AGE, GROWTH, AND POPULATION DYNAMICS OF COMMON BOTTLENOSE DOLPHINS (*Tursiops truncatus*) ALONG COASTAL TEXAS

A Thesis

by

RACHEL DAWN NEUENHOFF

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Christopher D. Marshall
Committee Members,	Bernd Würsig
	Antonietta Quigg
Head of Department,	Thomas Lacher

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ABSTRACT

Age, Growth, and Population Dynamics of Common Bottlenose Dolphins (*Tursiops truncatus*) Along Coastal Texas. (August 2009)

Rachel Dawn Neuenhoff, B.S., Texas A&M University at Galveston

Chair of Advisory Committee: Dr. Christopher D. Marshall

Common bottlenose dolphins (*Tursiops truncatus*) are apex predators and indicators of localized ecosystem health. Accurate characterization of population demography is crucial to parameter predictions. However, descriptions of age growth investigations of odontocetes are limited to the postnatal life. In contrast, the modeled scenario for terrestrial mammalian growth has been described along a continuum of pre- and postnatal data. Few age distribution data exist for the western Gulf of Mexico despite the fact that life tables enable demographic comparisons among populations. The objective of this study was to characterize age, growth, and population-level behavior of bottlenose dolphins along Texas. This objective was accomplished by two discrete studies: age analysis, and population-level behavior. Teeth from 290 stranded individuals were extracted for the purposes of age determination. Curvilinear models (the Gompertz and the von Bertalanffy) were fit to postnatal length-at-age data. Fetal age was determined for 408 suspected fetal length records using validated fetal growth trends and empirical measurements from late-term fetuses. Growth analysis indicated that a Gompertz model fit length-at-age data better than a von Bertalanffy model. A

postnatal Gompertz model explained less variation than a combined pre- and postnatal model (R^2 = 0.9 and 0.94 respectively). The absolute growth rate and rate of growth decay tripled with the inclusion of fetal length and age data. In the second study, life tables were constructed for 280 individuals. Survivorship curves, mortality rates, intrinsic capacity for increase, and the population growth rate were calculated. Bottlenose dolphin mortality did not differ significantly by sex or age class. Survivorship was best characterized by a type III curve. Analyses indicated no substantial increase (r = -0.07), and that the population is not replacing itself in the next time-step (λ = 0.93). Bottlenose dolphins conform to a number of eutherian mammalian trends: the production of precocial young, calving seasonality, and rapid fetal growth rate. Population level behavior suggests a population retraction possibly as a compensatory response to ecosystem perturbation rather than a population decline. Reproductive information will confirm population status and stability in the future. This study is the first to demonstrate a significant impact of cetacean fetal growth parameters on postnatal growth trajectory.

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CHAPTER I

INTRODUCTION

Background

Long-term observations of demographic patterns in populations of large predators such as common bottlenose dolphins (*Tursiops truncatus*, hereafter referred to as bottlenose dolphins) are important to efficient management and conservation efforts. In Sarasota Bay and surrounding waters, one of few investigations of wild bottlenose dolphins has yielded multi-decadal demographic data regarding calving season, length-at-birth, growth, maturity, and mortality (Read *et al.* 1993, Wells *et al.* 2004, Wells & Scott 1990, Wells *et al.* 2005), and underscores the value of long-term observations of age frequencies. For example, fluctuations in population parameters over time may indicate density compensatory responses, ultimately reflecting the population's proximity to its carrying capacity (Chivers & Myrick 1993), an important assessment for population management of long-lived animals.

Population parameters for terrestrial mammals are estimated by characterizing growth as a length, or weight-at-age, curvilinear function that includes pre- and postnatal life (e.g. Laird 1966b). Unfortunately, prenatal data are generally excluded from marine mammal growth curves due to the scarcity of

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This thesis follows the style of Marine Mammal Science.

embryonic and fetal specimens. For this reason, cetacean growth curves are exclusively postnatal, and model assumptions of residual normality and constant variance are usually violated. Therefore, parameter estimates must be interpreted with caution if a large proportion of the variation is unexplained, particularly for genetically structured populations (Eveson *et al*. 2007). Other useful tools in population studies are life tables, particularly for populations for which few distribution data are available. The advantage to creating life tables is that they are easy to construct, only require age information, and yield much population information such as age specific mortality rates, survivorship and age distribution (Krebs 1978, Krebs 1998).

In the present study, information from salvage material was used to investigate population parameters of bottlenose dolphins along the Texas coastline. First, a prenatal dataset was combined with a postnatal dataset to improve the fit of curvilinear growth models. Such methodologies are hypothesized to improve parameter estimates by explaining more variability, extending the growth curve back in time, and capturing the maximal growth rate; this will enable stronger inferences using data from salvage material. Second, postnatal age data were used to construct a time-specific life table to calculate survivorship, age distribution, and age-specific mortality for bottlenose dolphins along the Texas coast.

Geographic Distribution and Range of Bottlenose Dolphins

Bottlenose dolphins are perhaps the best known odontocete, and genetic stocks have been most intensively studied near the tropic and temperate regions (Baumgartner *et al.* 2001, Connor *et al.* 1992, Mead & Potter 1990, Mullin *et al.* 1994, Stolen *et al.* 2002, Turner *et al.* 2006, Wells & Scott 1990), although they also occur at higher latitudes (Mann & Watson-Capps 2005, Haase & Schneider 2001, Cockcroft & Ross 1990b). Most data on bottlenose dolphins come from the north and western Atlantic ocean (Barco *et al.* 1999, Mead & Potter 1990, Mullin & Fulling 2003, Weir *et al.* 2001), the northwest Mediterranean, the Spanish Mediterranean and the Straits of Gibraltar (De Segura *et al*. 2008, de Stephanis *et al*. 2008, Gannier 2006), the eastern Pacific ocean (Bräger & Schneider 1998, Morteo *et al.* 2004, Silber *et al.* 1994, van Waerebeek *et al.* 1990), the Indian ocean (Cockcroft *et al.* 1991, Cockcroft & Ross 1990b, Mann *et al.* 1999, Mann *et al.* 2007, Mann & Smuts 1999, Mann & Watson-Capps 2005), and more recently, the Gulf of Mexico (Baumgartner *et al*. 2001, Fernandez & Hohn 1998, Mattson *et al.* 2006, Read *et al*. 1993, Sellas *et al.* 2005, Turner *et al*. 2006, Wells *et al*. 2004, Wells & Scott 1990). The northwest Atlantic offshore population has been documented as far north as southern Greenland. Inshore bottlenose dolphins from the northwestern Atlantic exhibit a widespread distribution from Florida up to the northeastern coastline of North America (Curry & Smith 1997, Mead & Potter 1990). The eastern Pacific population has been reported as far south as Chile (approximately -30ºS, van Waerebeek *et al*. 1990).

Along the central Gulf of Mexico, bottlenose dolphins inhabit a depth range less than 1,100 meters and an average depth of 257 meters (Mullin *et al*. 1994). Individuals are rarely observed beyond the 750 m isobath (Baumgartner *et al*. 2001). Population parameters often differ by geographic region and comparisons become difficult due to regional variability, growth model choice, and fit.

Genetics, Morphology, and Stock Delineation

Initially, Atlantic bottlenose dolphin stock delineation was based upon size differences that were presumed to be a result of genetic divergence or morphological plasticity (Mead & Potter 1990). In general, very large individuals were believed to be from offshore stocks, and smaller individuals from inshore stocks. However, genetic analysis suggests incomplete stock structuring between populations in both ocean basins. Mitochondrial DNA base pair sequencing has revealed that inshore groups from the Atlantic and Gulf of Mexico were genetically more similar than their offshore counterparts (Curry & Smith 1997).

Within the Gulf of Mexico, some genetic structuring is also evident among inshore stocks. The offshore population may represent a founder stock from which inshore populations within the Gulf originated. Such an event might have occurred relatively recently (on the order of hundreds of years) and may explain why genetic resolution among stocks remains unclear (Sellas *et al*. 2005). Other research suggests regular gene flow between local populations as indicated by low sequence divergence (Dowling & Brown 1993). Such results indicate a fluid

inshore stock structure with similar sources of size variation.

Feeding Ecology

Bottlenose dolphins exhibit a wide niche breadth due to their ecological and social versatility (Connor *et al.* 2000). They are generalists, preying upon benthic and nektonic species, but are known to pursue a variety of pelagic fish and squid. Investigations from the western Atlantic ocean suggest that bottlenose dolphins have a high reliance on sciaenid fishes and prey detection by passive listening (Gannon & Waples 2004, Mead & Potter 1990). Active foraging can be a social or a solitary endeavor. It is influenced by spatial heterogeneity as well as vertical and oblique learning. In fact, social learning has a strong influence on niche partitioning (Mann *et al*. 2007). For example, observations of bottlenose dolphin communities from Shark Bay, Australia suggest that calves actively seek opportunities to inspect successful prey catches of genetically unrelated adults. This tactic may increase the repertoire of predatory tactics available through oblique learning in addition to predatory versatility required for large-scale ecological patchiness (Mann *et al.* 2007).

Reproduction

Historically, information about the reproductive biology of bottlenose dolphins has been limited by a lack of age information. Advancements in age determination have expanded the scope of longitudinal (Haase & Schneider 2001, Mann & Smuts 1999, Wells & Scott 1990) and cross-sectional studies (Cockcroft & Ross 1990b, Fernandez & Hohn 1998, Mattson *et al*. 2006, Read *et*

al. 1993, Sergeant *et al.* 1973, Stolen & Barlow 2003, Stolen *et al*. 2002, Turner *et al*. 2006). Males are sexually mature at approximately twelve years of age, while females mature between the ages of ten and twelve, but may begin breeding as early as age five (Connor *et al*. 2000, Sergeant *et al*. 1973). Despite speculation over seasonal parity of females, Sergeant *et al*. (1973) concluded that a female averages one *corpus albicantia* per year.

Along coastal Texas, bottlenose dolphins exhibit a diffuse calving peak in March (Fernandez & Hohn 1998). Females give birth to a 110 cm calf (Fernandez & Hohn 1998), an estimate consistent with other estimates for the Gulf of Mexico (Mattson *et al*. 2006, Stolen *et al*. 2002). Males and females exhibit natal philopatry (Connor *et al*. 2000), but males establish larger geographic ranges, presumably encouraging genetic exchange between open communities (Wells & Scott 1990).

Objectives and Hypotheses

In the present study, age and growth was characterized for bottlenose dolphins along coastal Texas. Growth parameters (initial growth rate, exponential decay, asymptotic length, length at birth) were estimated using a combination of pre- and postnatal data from stranded bottlenose dolphins. It was hypothesized that 1) fetal age can be estimated by using measurements from ultrasound images and skeletal indicators of maturity; 2) the inclusion of prenatal growth data change the trajectory of length-at-age growth curves, such that growth rate is higher, asymptotic length is achieved earlier, and the predicted

length at birth more accurately reflects observations in the wild; and 3) the proportion of overall variability previously observed in length-at-age growth curves would be reduced. The second objective of the study was to determine patterns of survivorship and mortality of bottlenose dolphins along coastal Texas. It was hypothesized that the 1) mortality rate would be the highest for calves (<2 years) but would sharply decline with age, and 2) the population of bottlenose dolphins is stable and exhibits a stationary age distribution. Suggestions are provided for improving analyses of marine mammal demographic data using minimalistic field collection techniques.

CHAPTER II

AGE AND GROWTH

Introduction

In Sarasota Bay, Florida, bottlenose dolphins have been documented to live up to fifty years (Hohn *et al*. 1989). Females typically outlive males by about five to ten years. Growth plateaus earlier in females, which reach sexual maturity before males (Stolen *et al*. 2002). With respect to length, there is no evidence of a pubertal growth increase in bottlenose dolphins, although some evidence suggests that individuals may increase more dramatically in girth during this time (Read *et al*. 1993). Sexual dimorphism has been detected in most regions globally, except for Shark Bay, Australia where no sex-based size dimorphism is evident. This may be related to the markedly smaller size of individuals that inhabit this area (Connor *et al*. 2000). Individuals in the western Atlantic are sexually dimorphic with respect to asymptotic length. Males are eight to twenty cm larger than females (Fernandez & Hohn 1998, Read *et al*. 1993, Stolen *et al*. 2002). In the present study, sexual dimorphism was investigated with respect to length and growth rates.

Bottlenose dolphins along the coast of South Africa exhibit an initial mass and length increase of 255 percent and fifty-seven percent, respectively, in the first year of life, before growth rates decline sharply (Cockcroft & Ross 1990b). Within the Gulf of Mexico, this dramatic growth period is evident in the

considerable length variability exhibited in early age classes (Fernandez & Hohn 1998, Mattson *et al.* 2006, Turner *et al*. 2006). This period of early growth coincides with a decline of early calf mortality rate particularly for calves of primiparous mothers (Connor *et al*. 2000, Wells *et al*. 2005).

Odontocete Age Determination

The term "growth layer group" (GLG) is used to describe one or more lamina apparent within a validated biological recording structure (e.g. long-bones, otoliths, teeth, posterior shell adductor muscle scars [PAMS], tympanic bullae) that represent a cyclical deposition (Chong *et al*. 2007, Garcia-March & Marquez-Aliaga 2007, Jackson 2007, Kilada *et al*. 2007, Klevezal 1980, Marmontel *et al*. 1996, Myrick & Cornell 1990, Shelton *et al*. 2006, Hohn *et al*. 1989, Hui 1980). Striations in the dentin of odontocete teeth were first investigated in striped dolphins, *(Stenella coeruleoalba*), and were presumed to correlate to age (Nishiwaki & Yagi 1953). Odontocete age is determined by thin-sectioning and staining a tooth in the buccal-lingual plane. The GLG boundaries present in the secondary and tertiary dentin beyond the neonatal line can then be observed and counted (Figure 1). When stained tooth sections are viewed with transmitted light microscopy, a single GLG is comprised of one broad opaque layer, followed by a narrower layer of variable stainability, referred to as the translucent layer (Myrick *et al* 1983). The boundary of the GLG is a thin opaque margin (Myrick *et al*. 1983, Perrin & Myrick 1980). Growth layer group deposition rate is inconsistent but represents a yearly average (Hohn *et al*. 1989) that has been

validated in short-beaked common dolphins, *(Delphinus delphis,* Gurevich *et al*. 1980*),* dusky dolphins*, (Lagenorhynchus obscurus,* Best 1976*),* and bottlenose dolphins by intramuscular tetracycline injections (Myrick & Cornell 1990). Since teeth from the central-most portion of the left or right mandibular ramus render the most accurate ages (Hui 1980), tooth collection is now standardized by exclusive tooth extraction from the center of the left mandibular ramus.

Modeling Length-at-Age Data

A number of dynamic growth models are used to analyze length-at-age data (Hohn 2002). The Gompertz growth model is the preferred prediction model for bottlenose dolphins in the western Atlantic ocean (Fernandez & Hohn 1998, Mattson *et al*. 2006, Stolen 1998, Stolen *et al*. 2002, Turner *et al*. 2006), although the von Bertalanffy model is also used for other delphinids (Rosas *et al*. 2003), and occasionally bottlenose dolphins (Cockcroft & Ross 1990). Despite this bias for the Gompertz model in the literature, the model does not fit all age classes equally well. An increased fit is sometimes observed when calves are excluded from analyses (Fernandez & Hohn 1998). Stolen (1998) noted the wide length variability of calves less than three years old, but retained this age class in analyses. Conversely, Read *et al*. (1993) reported that the Gompertz model fit most age classes well. However, in this study mother-calf pairs were necessarily excluded to reduce stress to live animals, effectively eliminating the problematic age class and possibly improving the fit of the model.

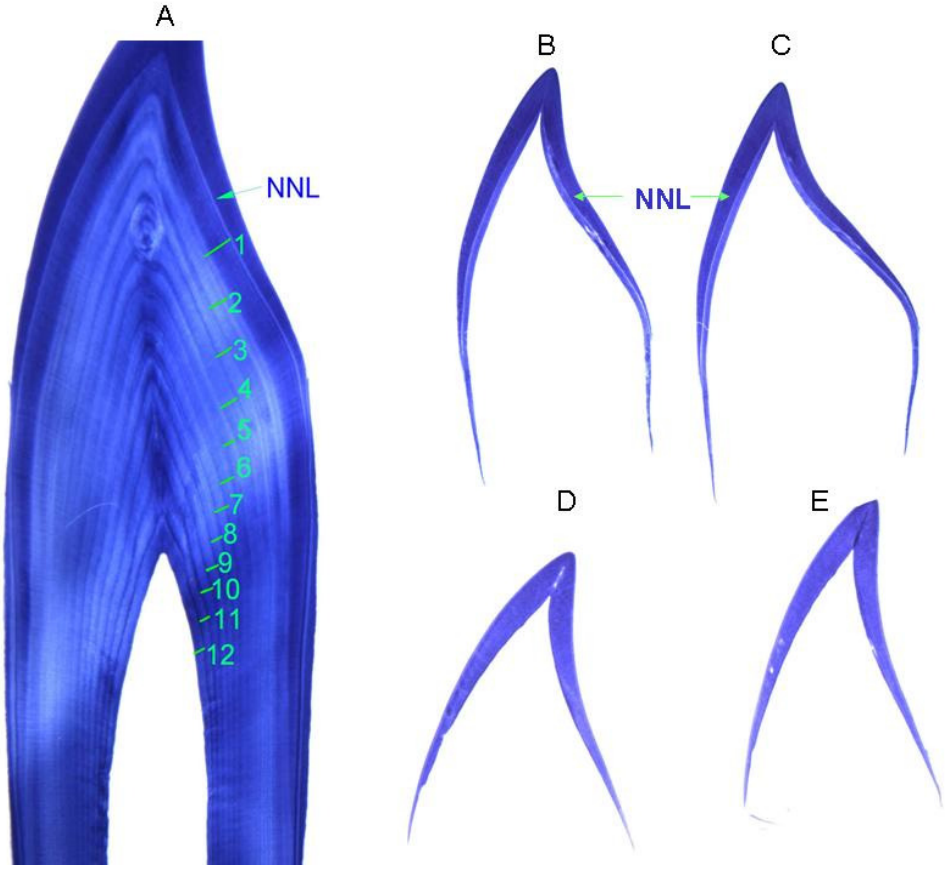

Figure 1. Growth Layer Group Analysis. An adult bottlenose dolphin tooth from a twelve-year-old individual. The thin, lightly stained, neonatal line is also present in the calf tooth (B, C), but not the fetal tooth (D, E). Subsequent GLG boundaries are marked and labeled by year.

Variability in one age class, especially in younger age classes, may indicate inadequate model choice (Campana & Jones 1992). Although maternal condition and investment have been suggested to explain this early life history variation, there has been virtually no attempt to investigate growth models with respect to variation in life history strategies. Therefore, this study included assessments of the statistical adequacy of using the Gompertz and von Bertalanffy growth models to analyze growth to test the hypothesis that the likelihood of these models is dependent upon an overall reduction of unexplained variability by including prenatal data in growth analyses.

Growth Models and Statistical Validation

Laird (1966b) used the Gompertz growth model to analyze the growth of terrestrial mammals, stating that the significant discrepancy between prenatal and postnatal growth rates necessitates the use of suitable dynamic growth models to describe mammalian growth. The Gompertz equation follows the form:

$$L_t = L_o e^{[G/g\ (1-\exp(-gt))]}$$

(Laird 1966a)

where L_t = the length at time t, L_o = total length at t = 0 (birth) and G/g = initial growth divided by the exponential rate of decay (Laird 1966b). The G/g term is sometimes referred to as k, the growth rate constant (Stolen *et al*. 2002), or b, the constant of integration (Fernandez & Hohn 1998). The curve can be fit if age

and length are known and the asymptote is estimated. The asymptotic length can be expressed by the following:

$$L_\infty = L_0 e^{G/g}$$

(Ricker 1979)

where L_∞ is the asymptotic length (Ricker 1979).

The second and less frequently used growth model to describe bottlenose dolphin growth is the von Bertalanffy model:

$$L_t = L_\infty (1 - e^{-G/g(t)})$$

(von Bertalanffy 1938)

Ricklefs (1967) assumed that the point of inflection of dynamic growth models occurs at t=0 and L_i (time and length at birth). This point along the curve is known as the "inflection parameter" (Fitzhugh 1975). Mammalian growth curves can be normalized by setting the inflection parameter to t=0 while its position along the ordinate varies (Laird 1966b). In a study of mammalian and avian intrauterine growth, birth often occurred *after* the attainment of maximal growth rate (Laird 1966a), underscoring the significance of the inflection parameter. By convention, the Gompertz model predicts the point of inflection at thirty-seven percent of the curve, while the von Bertalanffy model predicts the point of inflection at thirty percent (Zullinger *et al*. 1984). This makes the manipulation of the dataset in relation to the point of inflection an important note that is often overlooked.

The typical cetacean length-at-age curve is often displayed such that the scale does not suggest a point of inflection or the curve lacks any discernable point of inflection (Figure 2), and thus fails to conform to the underlying sigmoidal stipulation of the Gompertz model. The variability noted in certain age classes (Fernandez & Hohn 1998, Read *et al*. 1993, Stolen 1998) may be reduced by combining pre- as well as postnatal data, yet prenatal data are often precluded from cetacean length-at-age analyses.

Offspring Precociality and Growth Rate

Although Laird (1966a) stressed the influence of the inflection parameter, the maximal growth rate of each subject was forced to pass through t=0. Laird (1966b) conceded that upon closer inspection, the location of the inflection point among mammalian growth curves was variable, and speculated that this variability was linked to life history strategy choices in offspring development and parental care. This hypothesis was later expanded to the size-at-age growth of sixty-nine taxa of eutherian mammals, which were compared using a Chapman-Richards model to detect plasticity in growth trends (Gaillard *et al*. 1993). Each mammalian group was assigned a precociality index from zero to four (in order of increasing precociality) based upon a series of developmental and parental strategies. Among terrestrial mammals, precocial offspring exhibited maximal growth rates (curve inflection) before birth, whereas altricial offspring exhibited

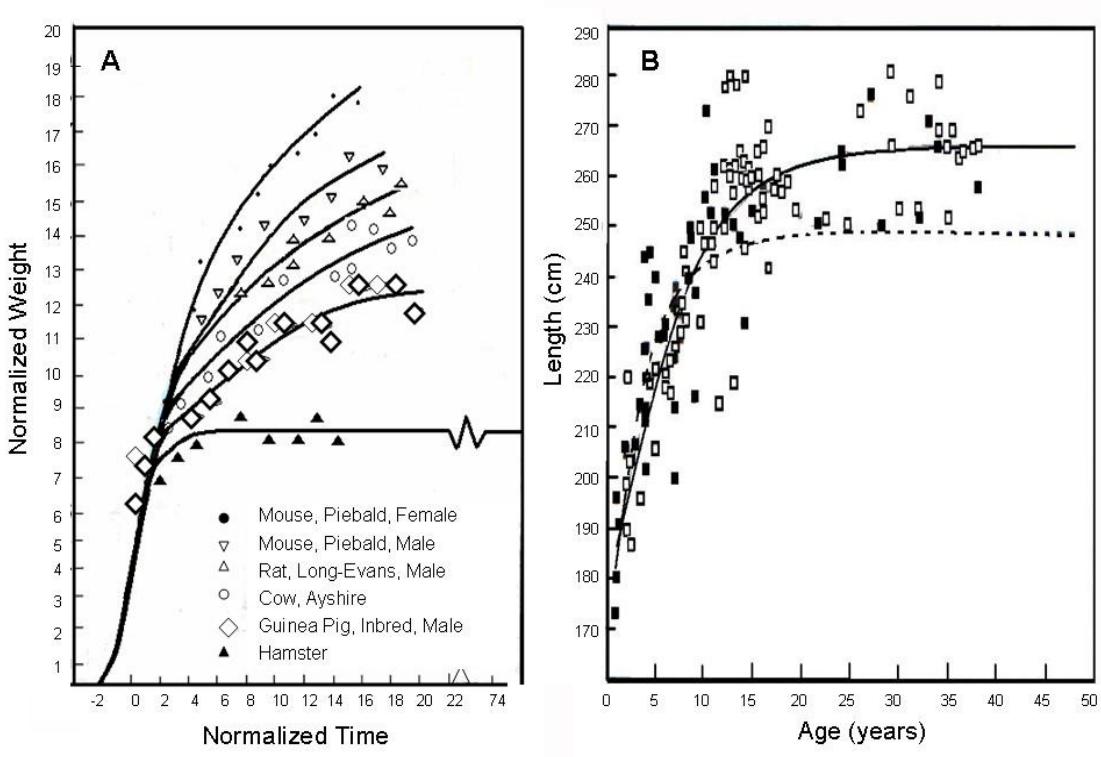

Figure 2. Mammalian Growth Analyses. Plot A displays weight-at-age Gompertz growth curves for five terrestrial mammals (Laird 1966a). Time (x-axis) is normalized to reflect the pre- and postnatal life of each animal and the inflection parameter has been forced to pass through zero. Plot B displays a length-at-age Gompertz growth curve for bottlenose dolphins (Read *et al*. 1993). Notice that the time scale does not extend into the prenatal life.

maximal growth rates after birth (Gaillard *et al*. 1997). On the precociality scale, cetaceans are given a score of three, based on four criteria of neonatal independence: thermoregulation, sensory ability, locomotion, and nutritional requirement (Derrickson 1992, Vaughan *et al*. 2000). Postnatal size-at-age growth functions fall into one of two categories: non-sigmoidal size-at-age functions (monotonic concave pattern) and sigmoidal size-at-age functions (Gompertzian pattern; Figure 3). Furthermore, Gaillard *et al*. (1997) encouraged workers to consider growth beginning from conception, not from birth, whenever possible to capture the point of inflection. It follows then that the growth trend of bottlenose dolphins from conception to birth and through adulthood would show a similar sigmoidal pattern exhibited by terrestrial mammals that produce precocial young. Therefore, an objective of this study was to analyze pre- and postnatal length-at-age data to test the hypothesis that the dynamic growth model choice and fit will improve using this comprehensive dataset (pre- and postnatal) to reduce overall unexplained variability and determine maximal growth rate.

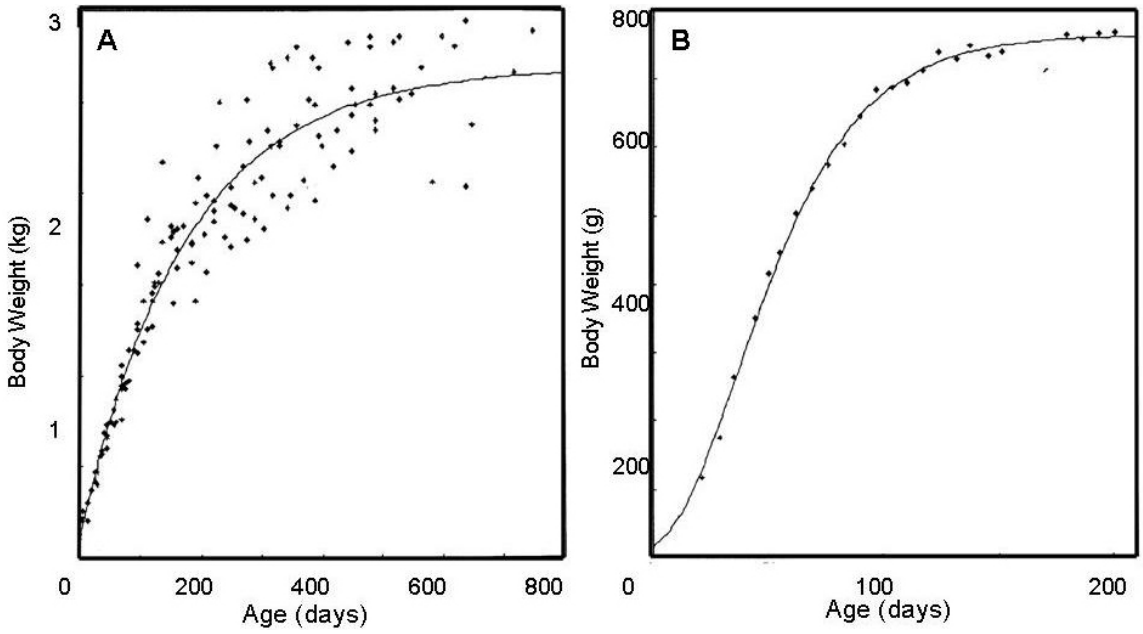

Figure 3. Monomolecular vs. Gompertzian Growth. Postnatal weight-at-age growth curves for two mammalian species that produce two types of offspring respectively: A. monomolecular growth pattern of precocial African brush-tailed porcupines (*Atherurus africanus*), and B. Gompertzian growth of altricial muskrats (*Ondatra zibitheca,* Gaillard *et al*. 1997).

Estimated Daily Growth as an Indicator of Prenatal Age

Huggett and Widdas (1951) first characterized mammalian intrauterine life as having two distinct growth patterns, the non-linear relationship (embryonic) and the linear relationship (fetal). Since information regarding cetacean growth rates was limited, these authors invited the investigation of fetal growth relationships in cetaceans. Later, investigators used whaling records to regress fetal length against the date of the death of the mother (Frazer and Huggett 1973). The authors concluded that a linear function best described cetacean fetal length-at-age in the latter part of pregnancy. The hypothesis has been tested for a variety of fetal mysticetes and odontocetes including blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*), sei whales (*B. borealis*), northern minke whales (*B. acutorostrata*), humpback whales (*Megaptera novaeangliae*), gray whales (*Eschrichtius robustus*), sperm whales (*Physeter macrorhynchus*), belugas (*Delphinapterus leucas*), harbor porpoises (*Phocoena phocoena*), bottlenose dolphins (Frazer and Huggett 1973), pilot whales (*Globicephala sp.,*Frazer and Huggett 1973; Rothery *et al*. 1995), Baird's beaked whales (*Berardius bairdii,* Kasuya 1977), and Tucuxi (*Sotalia guianensis,* Rosas *et al*. 2003).

Bottlenose dolphin gestation is approximately one year (McBride & Kritzler 1951, Urian *et al.* 1996). For cetaceans that exhibit a gestation greater than 200 days, the inception of fetal development in number of days since conception can

be estimated by the following ratio when length is regressed against gestational age:

$$100 t_0 / t_g = 10$$

(Frazer and Huggett 1973)

where t_o is the fetal age at the x intercept and t_g is fetal age at full term (Frazer & Huggett 1973). Fetal growth per day for bottlenose dolphins can then be calculated by the following equation:

$$\text{cm/day} = L_o/(365\text{-}t_o)$$

(Kasuya 1977)

where L_o is the length at birth and t_o is the first day of fetal development (Kasuya 1977). Critics argue that delineations based upon fetal length are oversimplified because they emphasize fetal stages and de-emphasize embryonic stages in which developmental progression establishes the context for rapid allometric growth (Sterba *et al*. 2000). Many workers consider length an inadequate index of gestational age, just as it is for postnatal individuals. Nonetheless, advances in artificial insemination programs have provided unequivocal knowledge of conception dates, and the broadened clinical applications for B-mode ultrasonography for marine mammal fetal growth charts have conclusively established the fetal growth trend with respect to gestational age (Stone *et al*. 1999, Williamson *et al*. 1990). Fetal bottlenose dolphin growth has been modeled by the expression,

Biparietal diameter (mm) = -0.408 (days before parturition) + 135.612

(Lacave *et al*. 2004).

Biparietal diameter is used rather than length due to the difficulty in obtaining accurate length measurements using ultrasound technology. However, it is possible to deduce length if the allometric relationship between biparietal diameter and length is known. The allometric law can be expressed as the following power function:

$$y = bx^{\alpha}$$

(Huxley 1936)

where y is the organ or structure of interest, x is the standard or the whole to which y is being compared, b is some initial growth index defined when x=1, and α is the proportional constant of growth (Huxley 1936). Therefore, if y (biparietal diameter) and x (length) are known from empirical observations of stranded perinates, and α is assumed to be approximately one (if fetal size-at-age is a linear function). The growth index, b is deduced by algebra,

$$b = y/x$$

and can be used to predict length or biparietal diameter when only one of the measurements are available. Therefore, an objective of this study was to collect empirical measurements of biparietal diameter and length from perinates stranded along coastal Texas to derive the growth index of these measurements.

Skeletal Maturational Indicators of Prenatal Age

Descriptions of postnatal maturational progression of the cetacean forelimb have provided accurate and accessible indicators of postnatal age, growth and maturity (Butti *et al.* 2007, Calzada & Aguilar 1996, Cozzi *et al.* 1985, Eales 1953, Galatius *et al.* 2006, Ogden *et al.* 1981). Ogden *et al*. (1981) developed a graded ossification scheme for odontocetes based upon the progression of secondary ossification centers primarily in the radius and ulna. Secondary ossification of the cetacean forelimb initiates proximally and proceeds distally, starting with the proximal humerus and ending with the distal phalanges. The eventual convergence of the diaphysis (bony shaft) and epiphysis (ends of the bony shaft) is divided into six stages in which the radioluscence between the epiphysis and diaphysis diminishes with fusion. For instance, it was estimated that the appearance of osseous bridges (stage four) within the distal epiphyses of the radius and ulna coincide with sexual maturity in Dall's porpoise (*Phocoenoides dalli*). However, the authors (Galatius *et al*. 2006) make no further recommendations to correlate ossification progression to chronological age.

Following the methodology outlined by Ogden *et al*. (1981), secondary ossification of the flipper bones was evaluated for Mediterranean striped dolphins (Calzada & Aguilar 1996). Unlike the postnatal striped dolphins in this study, no reference was made to the gestational ages of the five fetal dolphins included in the sample. However, secondary ossification in the flippers of these fetal

individuals was described in detail (Figure 4). In general, the proximal humerus was in an advanced state of ossification before birth while the epiphysis of the distal humerus was still active. The proximal radius and ulna were in developmental stages comparable to the distal humerus. In the distal radius and ulna, the epiphyses represented fifty to one hundred percent of the width of the adjacent diaphyses. The carpals and metacarpals exhibited only primary ossification. In smaller fetuses, some of the metacarpals (e.g. MI) lacked any observable ossification, and the appearance of secondary ossification of the metacarpals was variable. Phalangeal primary ossification was largely lacking in fetal striped dolphins. Observations of primary ossification can be correlated to chronology of ontogenetic shifts (Ogden *et al*. 1981), age of postnatal individuals (Calzada & Aguilar 1996), and the presence of derived characteristics (Galatius *et al*. 2006). Therefore, an objective of this study was to correlate ossification of the flipper bones in late-term prenatal bottlenose dolphins with gestational age.

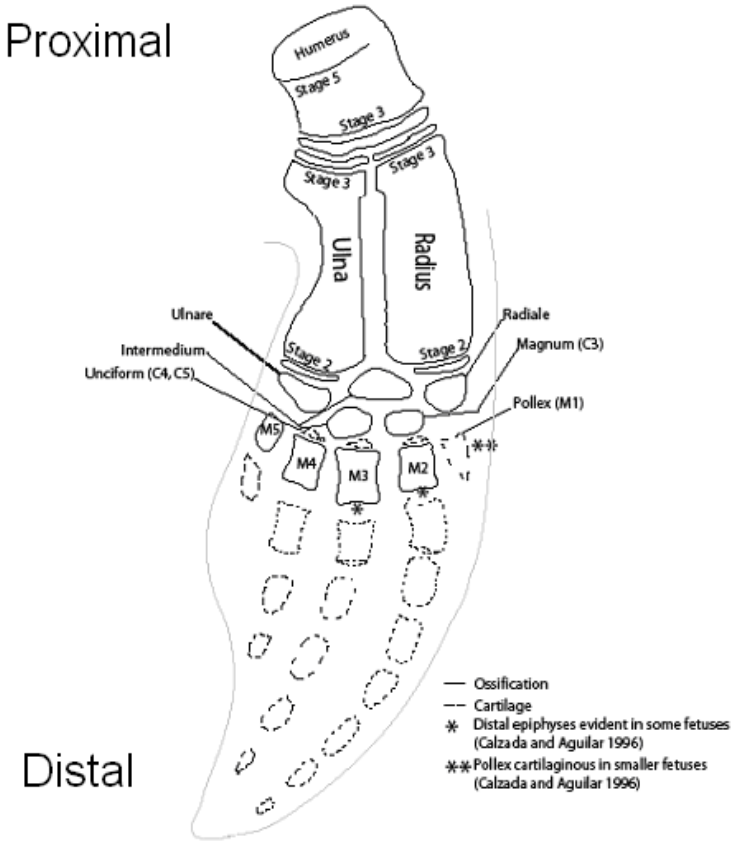

Figure 4. Ossification Patterns. Fetal progression of primary and secondary ossification (Ogden *et al*. 1981) for striped dolphins (Calzada and Aguilar 1996). The phalangeal formula is for bottlenose dolphins; 1,8,6,4,2 (Rommel 1990).

Objectives and Hypotheses

The objectives of this study were to 1) analyze postnatal growth of bottlenose dolphins using two length-at-age growth models, the Gompertz and the von Bertalanffy growth model to test the hypothesis that there is significant difference in the explanatory power of the Gompertz or the von Bertalanffy growth models. If differences existed, the model explaining the most variability, determined by the least-squares iteration, was used to make inferences on growth throughout the remainder of the study. 2) To establish a growth curve for males and females using the best fitting model to test the hypothesis that Texas coastal bottlenose dolphins are sexually dimorphic with respect to length. 3) To determine gestational age of fetal bottlenose dolphins using salvage material and ultrasound data from artificial insemination and captive breeding programs to test the following hypotheses: there is no significant difference in the fetal biparietal diameter among each pregnancy. If no significant difference was detected, biparietal diameter data generated from each pregnancy were pooled to generate a single regression line for biparietal diameter-at-age. Second, there is no significant difference between fetal ages estimated by allometric growth indices (*sensu* Huxley 1936) and predicted ages using the estimated growth per day (*sensu* Kasuya 1977). If a difference was detected between methods, the allometric relationship between biparietal diameter and length was used to age prenatal individuals. 4) Correlate skeletal maturation to gestational age according to the maturation-grading scheme of Ogden *et al*. (1981), to establish

a quantitative developmental series for prenatal bottlenose dolphins to test the hypothesis that there is no correlation between flipper skeletal maturity and gestational age. 5) Analyze pre- and postnatal growth of bottlenose dolphins stranded along the Texas coast using the least-squares Gompertz and von Bertalanffy growth model to test the hypothesis that a pre- and postnatal length-at-age growth model will not explain more variability than an entirely postnatal length-at-age model. 6) Determine if length at birth predicted from the best fitting postnatal length-at-age growth model differs from the length at birth predicted by the postnatal length-at-age model to test the hypothesis that prenatal length and age data do not affect model parameter estimates.

Methods

Animals

Three hundred twenty-one teeth were collected by volunteers from the Texas Marine Mammal Stranding Network from January 1991 to December 2007, and processed for aging by the investigator (RDN). Teeth were extracted from the left mandibular ramus, and stored in ten percent buffered formalin for twenty-four hours. Since there is a possibility that formalin can degrade to formic acid, the principle agent used for acid etching (Hohn 2002, Hohn *et al*. 1989), teeth were rinsed for an hour and stored dry immediately after fixation. In addition, perinatal heads (N=10), and flippers (N=8) were collected during March of 2008 from stranded individuals. Biparietal diameter was measured at random intervals from ultrasound images (N=5) during Atlantic bottlenose dolphin

pregnancies at Dolphin Quest, Bermuda. Measurements were collected by trainers, and subsequently approved by a licensed veterinarian. The measurements were then sent to the investigator for biparietal diameter-at-age analysis.

Postnatal Aging

Teeth were thick-sectioned using a low-speed Buehler Isomet saw (Buehler, Lake Bluff, IL) to obtain a two mm section of the central-most portion in the buccal-lingual plane. If the orientation of the tooth was unclear (i.e. the crown was broken off, or the tooth had excessive wear) the tooth was oriented by the trajectory of wear patterns and tooth width in the buccal-lingual plane. Occasionally, teeth were curved to such an extent that GLG's may have been lost if they were processed in the buccal-lingual plane. Buccal-lingually curved teeth were processed in the anterior-posterior (AP) plane with the caveat that GLG's would be less symmetrical than they would be in the buccal-lingual plane.

Once the tooth was correctly oriented and cut, the thick sections were decalcified using a rapid commercial decalcifier, RDO (Apex, Aurora, IL) for approximately seven to seventeen hours depending upon the age and degree of pulp cavity occlusion. Complete decalcification was determined by visual examination for opaque white areas (mineralization). Decalcified teeth were rinsed in tap water for six hours to remove excess RDO. Decalcified thick sections were thin sectioned at thirty μm on a circulating water freezing stage

(Physiotemp, Clifton, NJ) attached to a Lipshaw 80A sledge microtome using HistoPrep freezing media (Fisher Scientific, Fair Lawn, NJ).

On-center sections were stained in Mayer's hematoxylin for sixty-five minutes, then "blued" in dilute ammonia for one minute. Sections were floated onto five percent gelatin coated slides. Slides were warmed on a hot plate on low heat for less than one minute to ensure that each stained section adhered to the slide. Sections were dehydrated, cleared, and coverslipped with Eukitt (Electron Microscopy Sciences, Hatfield, PA). Slides were allowed to air dry before examination under a Nikon Eclipse E400 light microscope (Nikon Instruments, Inc., Melville, NY).

Gestational Aging

To date, there is no validated method for aging stranded perinates. However, personnel at captive animal facilities keep records of known conception dates and a number of growth measurements as part of artificial insemination programs for the purpose of parturition date estimation. Data include approximate conception dates, birth dates, thoracic dimensions (Th), and biparietal diameter measurements from ultrasound images. Total length is never collected from ultrasound images due to imaging constraints. However, total length measurements are commonly recorded for stranded individuals recovered by Texas Marine Mammal Stranding Network (TMMSN) personnel. Therefore, fetal salvage material collected during one stranding season was used in

conjunction with ultrasound data (Figure 5) to investigate prenatal growth relationships.

Stranded perinates were confirmed fetuses or early postnatal if they met a set of field criteria outlined in Table 1. The left flipper (inclusive of the scapula) and skull were taken from each stranded perinate for radiographic imaging, determination of biparietal diameter, and assessment of ossification patterns in the bones of the forelimb. The law of allometry was used to derive a mean growth index (b) for perinatal biparietal diameter to length (BPD/length). Next, length records (N=408) from individuals suspected to be fetal at the time of stranding (range forty-four cm to 114 cm) were retrieved from the TMMSN database. These previously recorded lengths were multiplied by the mean growth index derived from salvage material to predict the biparietal diameter of each individual. Age was estimated using the best-fit regression equation of biparietal diameter at known gestational age of five (N=5) individuals detected by ultrasound as part of captive breeding programs. Ages and lengths were analyzed using the least squares Gompertz and von Bertalanffy growth models.

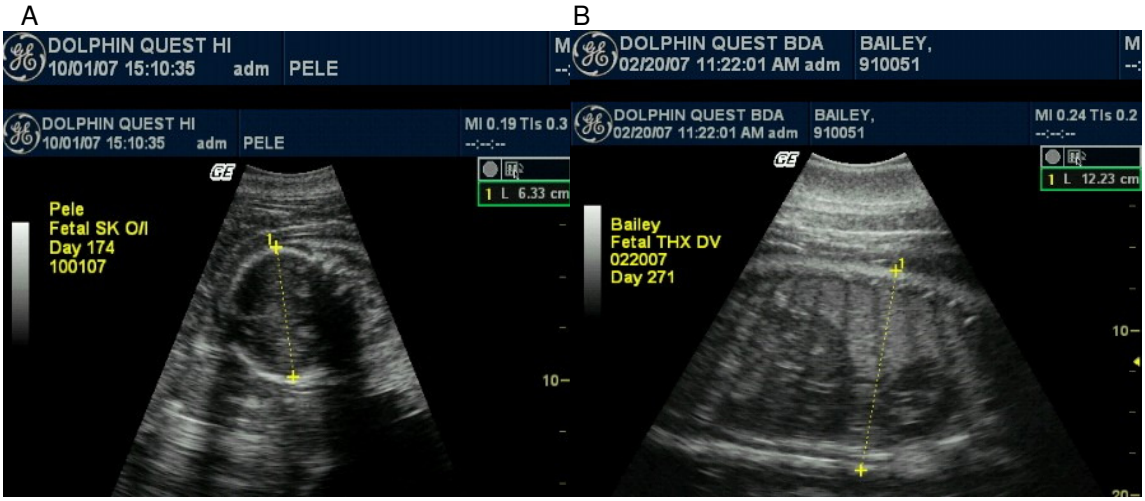

Figure 5. Ultrasonic Imaging. Ultrasound images taken from pregnant females as part of the artificial insemination program at Dolphin Quest, Bermuda. A: fetal biparietal diameter, B: fetal thoracic depth.

Table 1. Developmental Field Criteria. The following variables were used to classify stranded individuals as fetal or early postnatal individuals.

Feature	**Time of formation/diminishment**
Presence of rostral vibrissae	Form at stage 8 in utero (Sterba *et al*. 2000) Diminish twenty-two days postnatal (Cockcroft & Ross 1990a)
Teeth erupted	Less than six weeks postnatal (McBride & Kritzler 1951)
Less than 100 cm in Length	Based on predicted length at birth of 110 cm (Fernandez and Hohn, 1998)
Presence of true fetal folds	Diminish sixty-two days postnatal (Cockcroft & Ross 1990a)
Umbilicus healed	Twenty-two days postnatal (Cockcroft & Ross 1990a)

Radiology

Flipper radiographs were taken of flippers (N=8) using a Cabinet Faxitron on Kodak X-OMAT V 10”X12” film at the University of Texas Medical Branch in Galveston, Texas. The left flipper was disarticulated at the glenohumeral joint and frozen prior to radiography. Flippers were radiographed in the dorsal plane of the forelimb. This orientation exposes the maximal area of active forelimb bone formation and is the commonly adopted orientation for flipper radiographs (Eales 1953, Galatius *et al*. 2006). Secondary ossification of the radius, ulna, carpals, metacarpals, and phalanges were graded using the methodology of Ogden (1981). A flipper index (FI) was assigned by summing up the maturational scores of secondary ossification of each skeletal element for each forelimb following the methodology from Hui (1979). The FI was then compared to the approximated gestational age of each animal.

In addition, radiographs of perinatal bottlenose dolphin heads from stranded animals (Figure 6) were taken at the Texas A&M University College of Veterinary Medicine (Small Animal Clinic Radiology College Station, TX). The head from each individual was frozen and radiographed in the horizontal plane. Secondary ossification and biparietal diameter were measured directly from radiographic images using Image J 1.40g (Wayne Rasband, National Institutes of Health, USA).

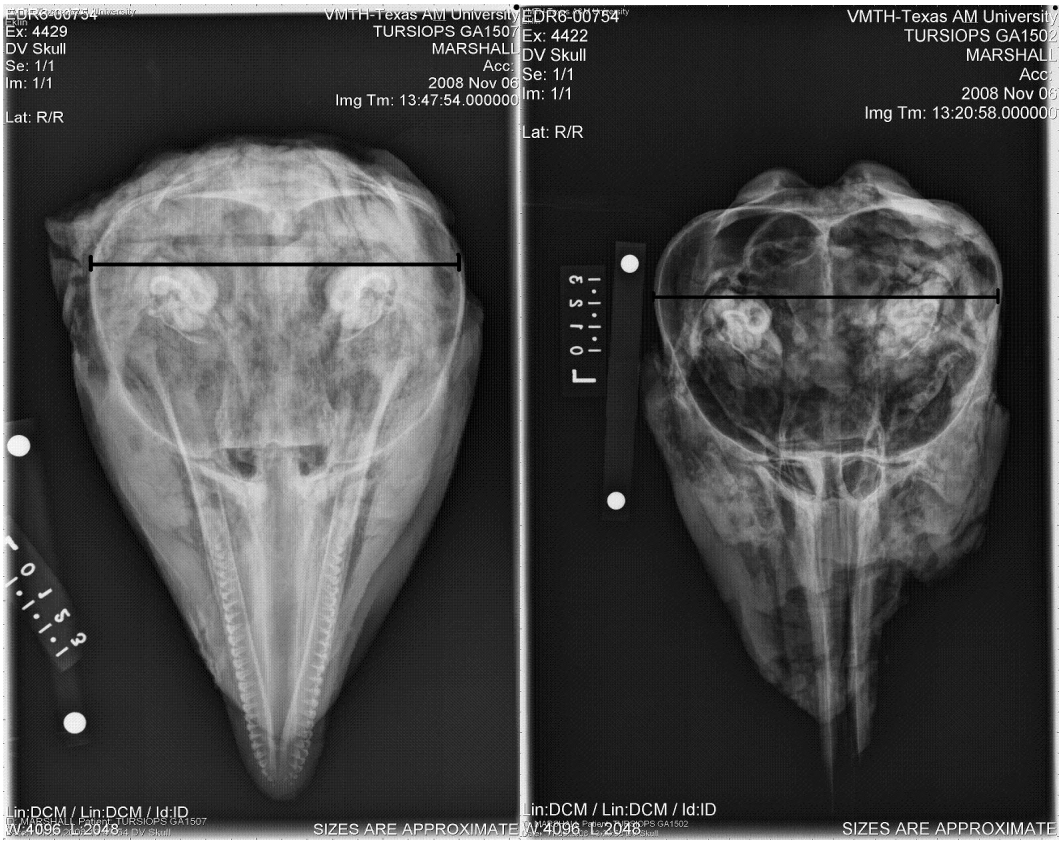

Figure 6. Radiographic Imaging. Two radiographic images taken of fetal bottlenose dolphin skulls. Biparietal diameter was measured (indicated by the black bar) at the widest point of the skull. Measurements were taken from the outer wall of the skull to the inner wall on the opposite side of the skull. This approach was used to maintain consistency with measurements taken from ultrasound images.

Length at Birth

Predicted length at birth values were compared among the best-fitting postnatal and the pre- and postnatal models. Once each model predicted a length-at-birth for each respective sample, a logistic curve was fit to the binomial condition of being either fetal or non-fetal as explained by length (*sensu* Danil and Chivers 2007). Individuals were classified as fetal based upon their age determined by GLG analysis or estimated gestational age. Individuals were classified as non-fetal if GLG analysis indicated the postnatal condition, and the individual was less than one year of age. The inflection point along the fitted logistic curve indicated median overlap of fetal and non-fetal length, and was taken to be an alternative measure of length-at-birth.

Analyses

Postnatal ages were estimated to the nearest tenth of a year. Estimations were made in the blind to the reader (necropsy reports were not reviewed until after age was estimated) to assure consistency and reduce bias. Two readers (Rachel Neuenhoff and Dr. Christopher D. Marshall – Texas A&M University) read each tooth three times. Each respective reading was spaced at least one day apart. If disagreement of perceived age existed, a fourth reading took place, and the average of the three nearest readings was taken as the actual age. The coefficient of variation was calculated among the readers. A third reader (Megan Stolen – Hubbs Seaworld Research Institute) read a majority of the teeth in order to validate the aging protocol utilized for this study.

Gestational age and skeletal indices were calculated using Microsoft Office Excel 2003. Regression analyses, residual analyses and ANOVA's were conducted using SPSS 14.0 (SPSS, Chicago, IL). Postnatal lengths and ages were analyzed with Gompertz and von Bertalanffy growth models using MATLAB R2007b (Mathworks, Natick, Massachusetts) from custom, curve-fitting code (Emily Kane). Each model was assessed by the coefficient of determination. The best fitting, least-squares model was used to compare differences in growth analyses using a postnatal length-at-age dataset and another that included pre- and postnatal data. Length-at-age curves were evaluated using a maximum likelihood least squares iteration. The logistic point estimate of length at birth and bootstrap analysis were conducted in "R" 2.8.1.

Results

Sample Demographics

Two hundred ninety teeth were successfully processed for aging. Three of these could only be estimated to a minimum age. Another thirty-seven were processed and determined to be fetal, and could not be accurately aged from the teeth. Eighteen individuals lacked length entries in the stranding database. These limited cases were usually due to decomposition or scavenging by animals before the carcass was recovered that prohibited accurate length measurements. This provided two hundred thirty-two postnatal lengths and ages. Initially, analysis indicated seventeen percent inter-reader variation. However, the most variable discrepancies were observed between the fetal and

neonatal age classes. Occasionally, a fetal tooth section exhibited a neonatal line, and consequently the animal was incorrectly placed in the neonatal age bin. When these cases were discarded from the analysis, the coefficient of variation decreased to ten percent.

The age distribution of bottlenose dolphins was left skewed (Figure 7). Neonates (postnatal individuals confirmed to be less than one year) made up twenty-three percent of the postnatal sample. This percentage is consistent with previous estimates (Fernandez & Hohn 1998, Stolen & Barlow 2003). Calf vulnerability immediately following parturition is thought to explain the high percentage of individuals that represent this age class. The calving season is deduced by the stranding frequency of neonates. Stranding patterns of near-term and neonatal individuals indicate that most calving occurs in March and begins to diffuse in April and May. Two of the December stranding records exhibited discrepancies between the aged tooth and the length record. These two neonates were recorded to be over 200 cm long and were discarded from the frequency distribution.

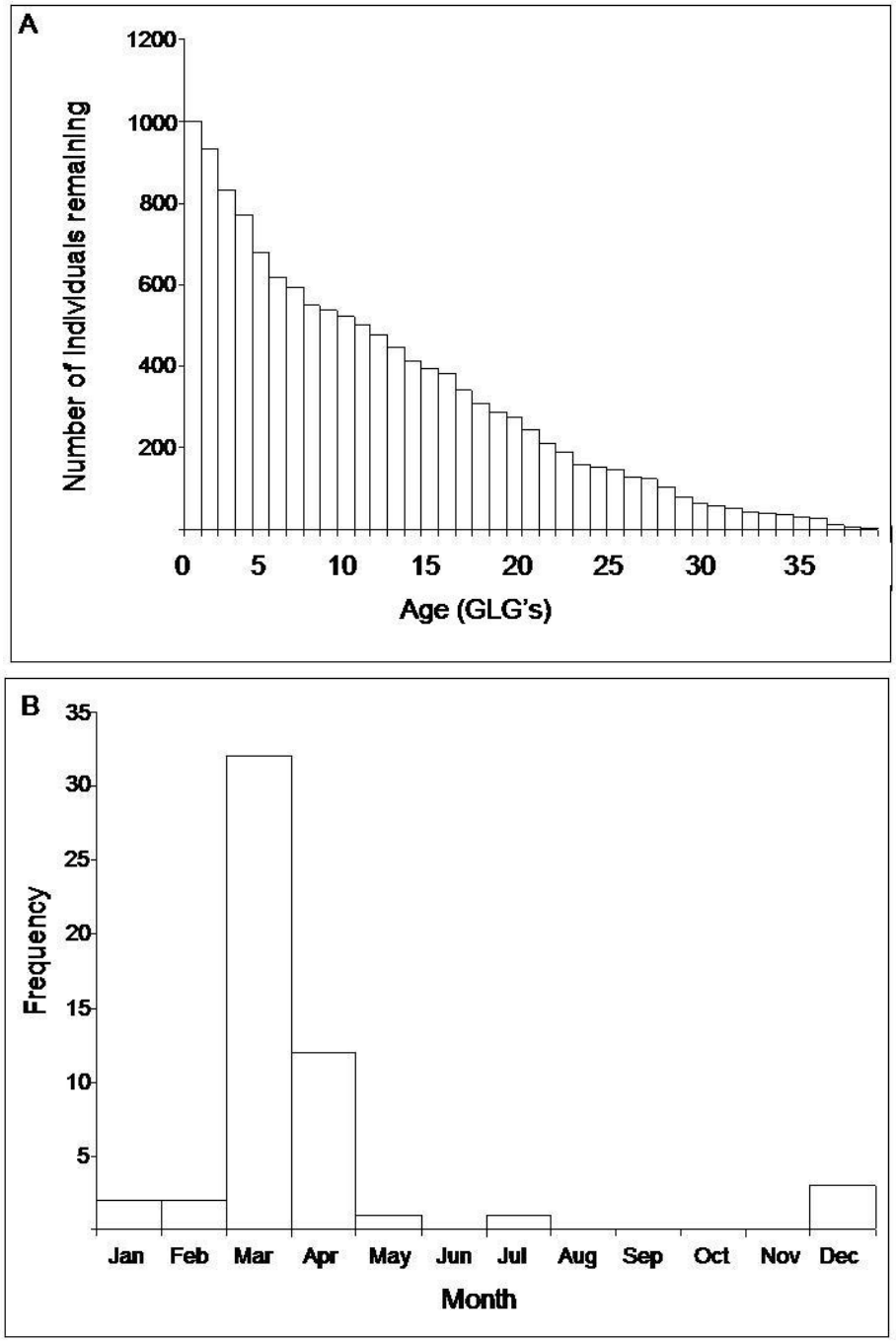

Figure 7. Stranding Frequency Distributions. Age distributions of bottlenose dolphins along coastal Texas. A: Ages from 290 individuals were confirmed by GLG analysis. B: Fetal and neonatal stranding frequencies by calendar month.

Postnatal Growth Analysis

The Gompertz and the von Bertalanffy models were ran until they each converged upon the least-squares iteration (Table 2). The von Bertalanffy was rejected on the basis of poor fit (Figure 8). Gompertz residual analysis indicated thirteen possible outliers that were subsequently discarded from further analyses. The postnatal Gompertz model met the assumption of homoscedasticity but residual distribution was non-normal. As expected, the Gompertz growth model underestimated asymptotic length, so adult length was fit by hand by plotting a set of Gompertz conversion factors against age (*sensu* Ricklefs 1967).

The results of least-squares Gompertz growth curves fit to male and female length-at-age data are shown below (Figure 9 and Table 3). The models exhibited good fit to both female and male length-at-age data. Female length-at-age residuals exhibited homoscedasticity while male length-at-age residuals did not. Both models underestimated the asymptotic length and so these values were also fit by hand. Length-at-birth was not different between males and females, nor was the growth rate constant. Females reached their asymptotic length before males by approximately two years. However, male growth persisted beyond female asymptotic length. This is explained by the higher initial female growth (G) and rate of growth decay (g).

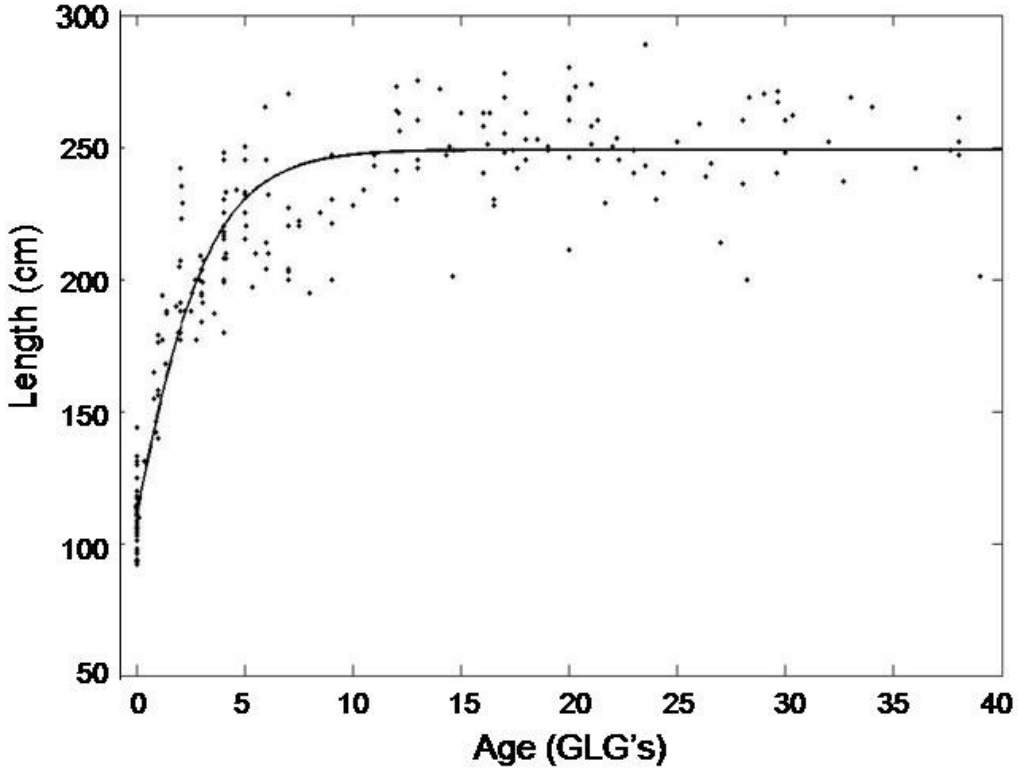

Figure 8. Postnatal Gompertz Model Fit to Length-at-Age.

Table 2. Length-at-Age Model Parameters. Postnatal growth parameters predicted by each model, where G is absolute growth, g is the exponential rate of growth decline, L_0 is length at birth, and L_∞ is the asymptotic length. The hand fit asymptote for the Gompertz growth model is reported in parentheses.

Curve	**R^2**	**G/g (k)**	**G**	**g**	**L_0**	**L_∞**
Gompertz	0.9	0.81	0.38	0.47	111 cm	249 (267) cm
Von Bertalanffy	0.77	0.74	0.35	0.47	- -	245 cm

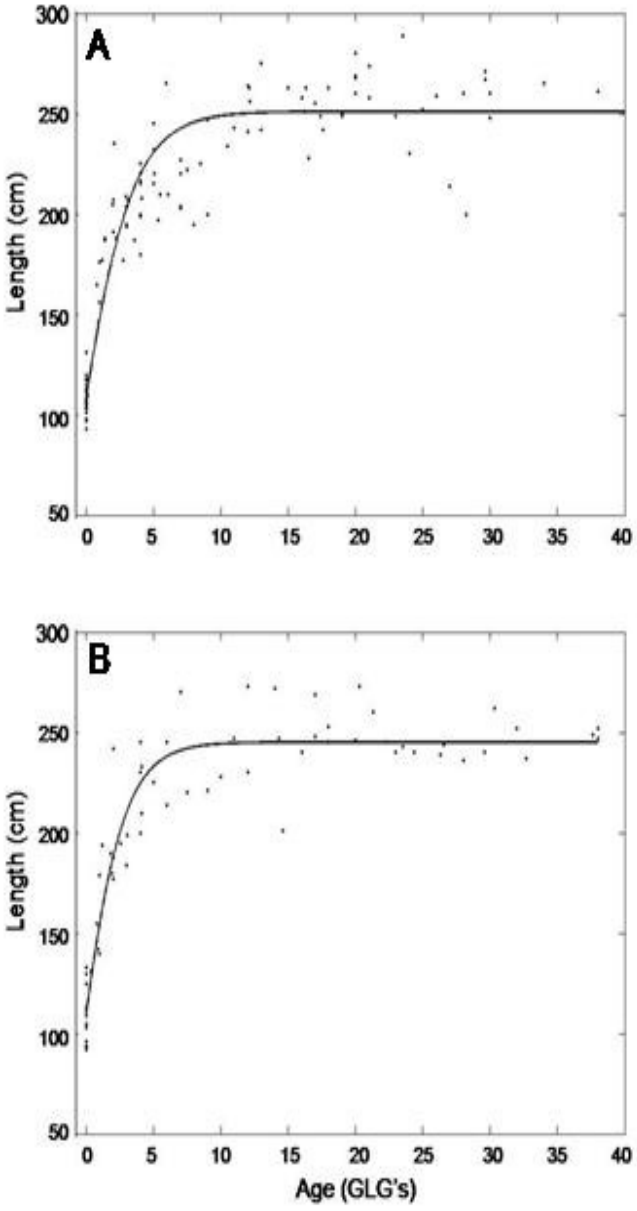

Figure 9. Male and Female Postnatal Model. Least-squares Gompertz growth curves fit to an exclusively postnatal female dataset (A) and an exclusively postnatal male dataset (B).

Table 3. Sex-Specific Postnatal Growth Parameters. Gompertz growth parameter estimates of fitted female and male datasets. The hand fit asymptote is reported in parentheses.

Curve	**R^2**	**G/g**	**G**	**g**	**L_0**	**L_∞**
Gompertz (Male)	0.91	0.84	0.38	0.46	109 cm	251.1 (280) cm
Gompertz (Female)	0.91	0.8	0.44	0.55	110.2 cm	245.2 (265) cm

Fetal Age and Growth Indices

Ultrasound data from artificial insemination programs yielded morphometric data from five pregnancies. A set of fetal measurements was recorded (a minimum of five and a maximum of eight) at different times over the course of each pregnancy. A one-factor ANOVA summarized in Table 4 demonstrated no significant difference in biparietal diameter-at-age of the five fetuses so the data were pooled for regression analysis (Figure 10). The analysis was significant at the $p<0.002$ level, and regression assumptions of normality ($p>0.02$) and homoscedasticity ($p>0.05$) were upheld.

The allometric growth indices calculated for each radiographed perinate skull are given below (Table 5). The mean index (0.114) was then used to convert the four hundred thirty-six suspected fetal length records retrieved from the TMMSN database to biparietal diameter for the purposes of gestational aging. One length record was not included because it was estimated less than thirty-seven days of gestation. This is near the embryonic period of gestation,

which is dictated by a non-linear growth process that Huggett and Widdas proposed (1951) would be best explained by an exponential growth function. However, embryonic characterizations of growth were outside the scope of the present study.

Table 4. Ultrasound Measurements. One-factor ANOVA for thirty-two biparietal diameter measurements taken from ultrasound images of five fetuses carried to term.

Groups	**Count**	**Sum**	**Average**	**Variance**		
Luna	8	80.23	10.03	7.76		
Bermudiana	5	48.57	9.71	3.13		
Nea	5	51.12	10.22	7.40		
Tatum	7	63.44	9.06	7.13		
Lily	7	58.14	8.31	5.77		
Source of Variation	**SS**	**Df**	**MS**	**F**	**p-value**	**F crit**
Between Groups	16.21	4	4.05	0.63	0.65	2.73
Within Groups	173.82	27	6.44			
Total	190.04	31				

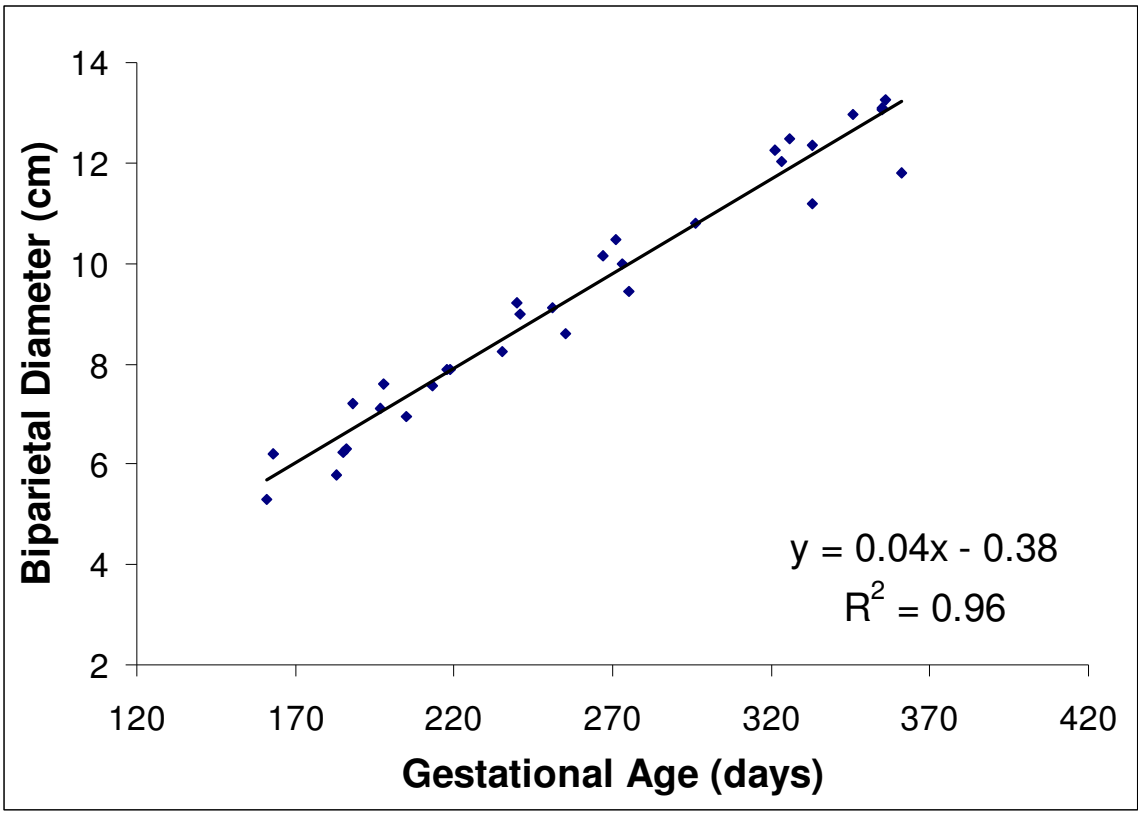

Figure 10. Biparietal Diameter vs. Gestational Age. Regression for fetal Atlantic bottlenose dolphins detected by ultrasound during pregnancies (N=5) conceived by artificial insemination.

Table 5. Calculated Fetal Growth Indices.

Regional Tag	BPD	Length (cm)	Alpha	Growth index
GA1473	11.46	110	1	0.10
GA1492	12.66	109	1	0.12
GA1496	12.64	112	1	0.11
GA1498	12.72	103	1	0.13
GA1501	12.95	108	1	0.12
GA1502	12.91	112	1	0.12
GA1504	11.36	104	1	0.11
GA1505	12.85	104	1	0.12
GA1507	11.43	102	1	0.11
PA756	11.77	110	1	0.11
			MEAN	**0.11**

The estimated biparietal diameter values were used to estimate gestational age based on the equation of the best fitting regression of fetal biparietal diameter and known gestational age:

$$\text{Gestational Age (days)} = (bx + 0.3774)/0.0376$$

A variation of the equation was used to express age in units of one year for the context of the growth model:

$$\text{Age} = (365 - (((0.114382 * \text{Fetal Length}) + 0.2553)/0.0371))/365$$

Based upon the previously predicted value of 110 cm (Fernandez and Hohn 1998) and the value predicted by the aforementioned fetal model at 365 days of gestation (116.6 cm), a the gestational age of all individuals that measured less than 116 cm was estimated. The estimated gestational ages were compared to gestational ages predicted using the methodology of Kasuya (1977) using an independent, two-sample t-test. Because ages predicted by allometric growth indices were significantly different from those predicted simply from average growth per gestational day, fetal allometric relationships (BPD/length) were used to estimate gestational age in further analyses.

Skeletal Indicators of Fetal Age and Growth

Eight fetal flippers were imaged and scored based on secondary ossification patterns. Each score was paired with its estimated gestational age based upon the negative allometric relationship between biparietal diameter and length (0.114). The results of a regression analysis are given in Figure 11. Analysis indicated a large proportion of unexplained variability, and a weak

correlation (r = 0.67) between ossification score and gestational age. Mean score, proportion of ossified elements, and appearance of cartilaginous elements failed to produce any stronger correlations to gestational age.

Pre- and Postnatal Age and Growth

Fetal lengths and ages were included with the postnatal length-at-age dataset, and the Gompertz growth model exhibited a better fit to the length-at-age data (Figure 12). Growth model parameters of each fitted model to each dataset (postnatal and the pre- and postnatal, respectively) are summarized in Table 6. Age at asymptotic length decreased, from approximately twelve years in the postnatal model to approximately six years in the combined pre- and postnatal model. In addition, the pre- and postnatal model underestimated asymptotic length by more than thirty cm. However, the fit of this model was far better at the lower end than the upper end of the growth spectrum. Interestingly, the initial growth rate (G) and the exponential rate of growth decay (g) both increased significantly when fetal data were included, but because both variables increased in the same relative proportions to one another (each roughly tripled), the growth rate constant (k) remained similar between both the postnatal and the pre- and postnatal growth curve.

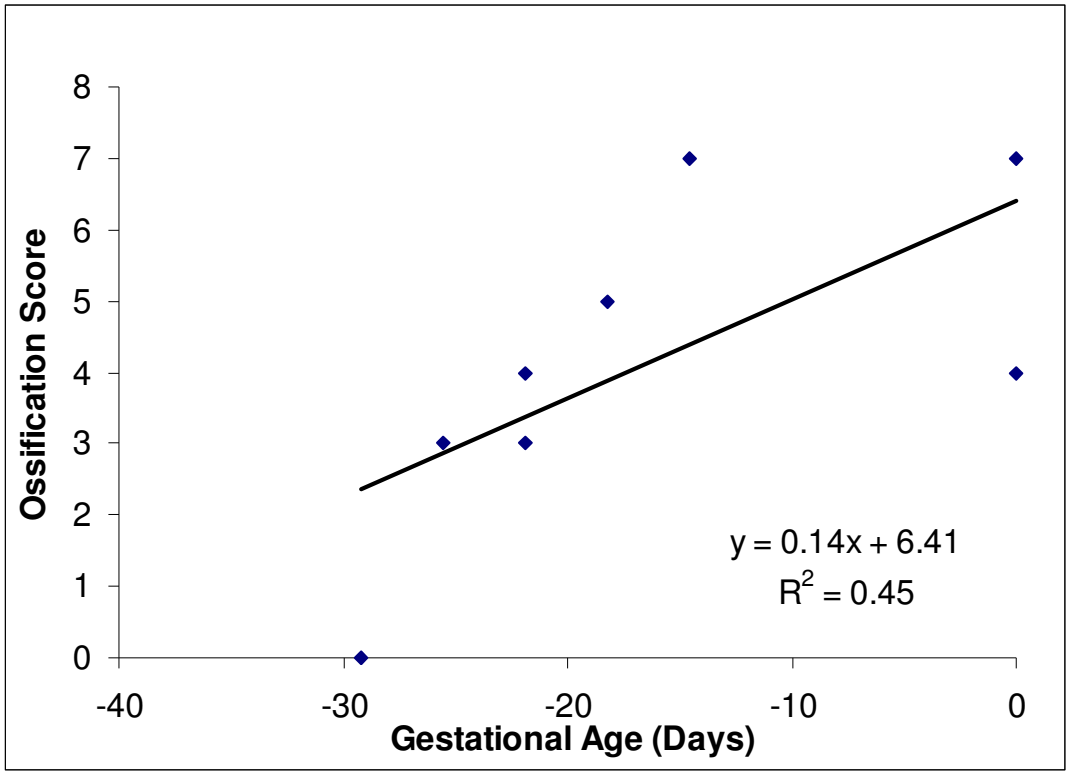

Figure 11. Ossification Score vs. Gestational Age.

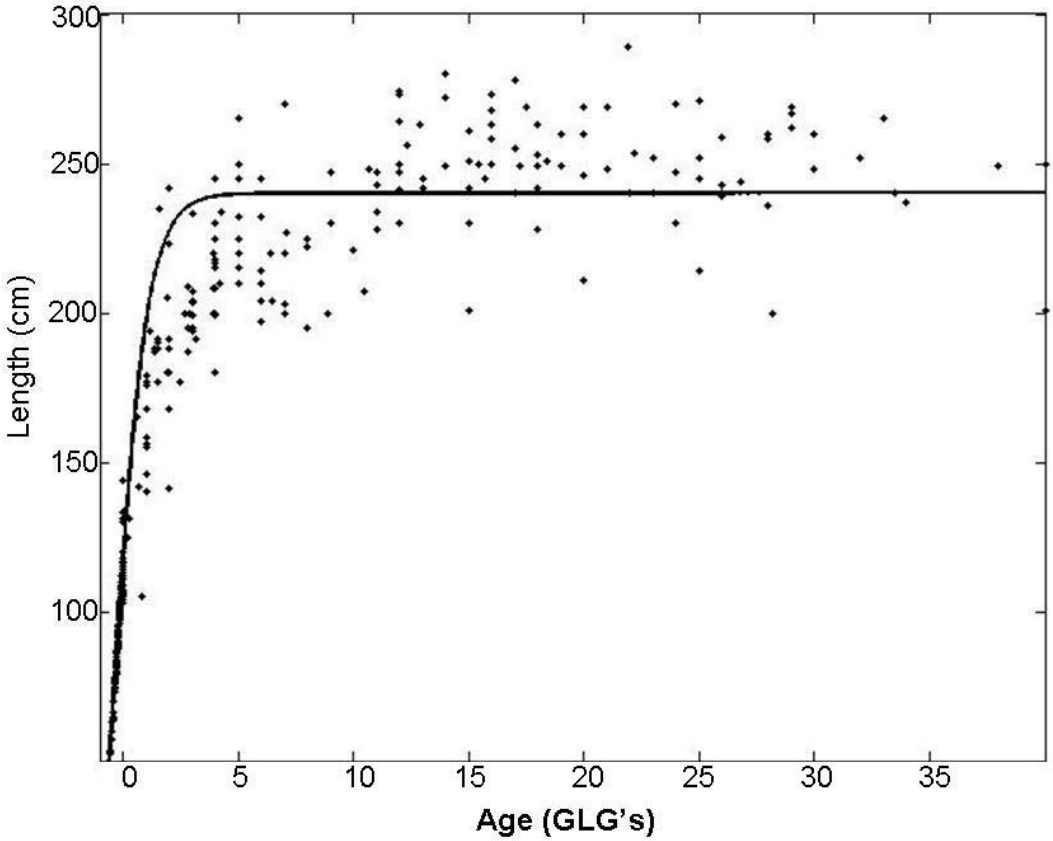

Figure 12. Pre- and Postnatal Model.

Table 6. Comprehensive Summary of Predicted Growth Parameters. Gompertz growth parameter estimates for the fitted pre- and postnatal dataset.

Curve	**R^2**	**G/g**	**G**	**g**	**L_0**	**L_∞**
Gompertz (Postnatal)	0.9	0.81	0.38	0.47	111 cm	249 (267) cm
Gompertz (Pre-/Postnatal)	0.94	0.72	0.99	1.4	116.3 cm	238.4 (270) cm
von Bertalanffy (Postnatal)	0.77	0.74	0.35	0.47	- -	245
von Bertalanffy (Pre-/Post)	0.66	0.28	-0.01	-0.03	--	254.3

Gompertz growth models were fit to female and male pre- and postnatal length-at-age data. Fetal male and female lengths and ages were combined for each curve because differences in growth regimes do not manifest until well after birth (Fernandez and Hohn 1998). The best-fit Gompertz growth models for pre- and postnatal length-at-age are provided below (Figure 13). The fits of both curves improved slightly, and the growth rate constants decreased (Table 7). The absolute growth rates and rates of growth decay nearly tripled. The similarity of male and female growth parameters in these cases reflect low variation between the two sexes during the intrauterine life. The length-at-birth values for males and females increased dramatically in the pre- and postnatal model but did not differ by sex.

Length-at-birth

Length at birth changed markedly with the inclusion of prenatal data, from 111cm to 116.3 cm. The results of a logistic model fit to a binomial distribution are summarized in the plot below (Figure 14). Fetal and neonatal lengths demonstrated observable overlap. However, the fitted mean probability (0.5) indicated that the point fit length-at-birth was approximately 114.7 cm. This estimate agrees with the Gompertz pre- and postnatal model prediction of 116.3 cm and supports the hypothesis that a pre- and postnatal length-at-age model predicts length at birth more precisely than an exclusively postnatal length-at-age model.

Discussion

Postnatal Growth Analysis

As predicted, the Gompertz growth model explained more variation than the von Bertalanffy growth model. The parameters predicted from the least-squares Gompertz growth model are consistent with parameters predicted for other regions (Table 8). Non-constant variance indicates that length is a poor measure to use to estimate age. Length may be more useful to describe growth processes, which may be of greater conservation and management concern than age prediction. Parameter values reported by Turner *et al*. (2006) and Fernandez and Hohn (1998) represent length-at-age curves generated for coastal Texas, and are similar for values reported for the Indian River Lagoon

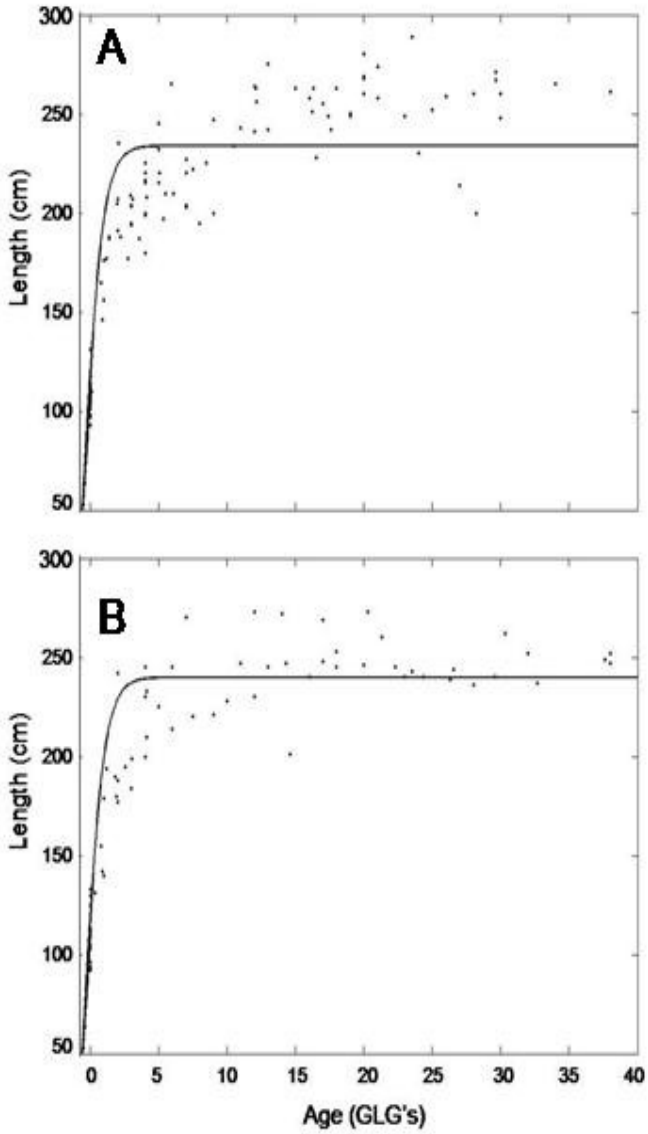

Figure 13. Pre- and Postnatal Male and Female Models. Least squares Gompertz growth models of pre- and postnatal female (A) and male (B) length-at-age data.

Table 7. Comprehensive Summary of Male and Female Growth Parameter Estimates.

Curve	**R^2**	**G/g**	**G**	**g**	**L_0**	**L_∞**
Male (Postnatal)	0.91	0.84	0.38	0.46	109 cm	251.1 (280) cm
Gompertz (Female)	0.91	0.8	0.44	0.55	110.2 cm	245.2 (265) cm
Male (Pre-/Postnatal)	0.95	0.7	0.98	1.4	116.3 cm	234 (265) cm
Female (Pre-/Postnatal)	0.94	0.72	0.99	1.4	116.3 cm	238.4 (265) cm

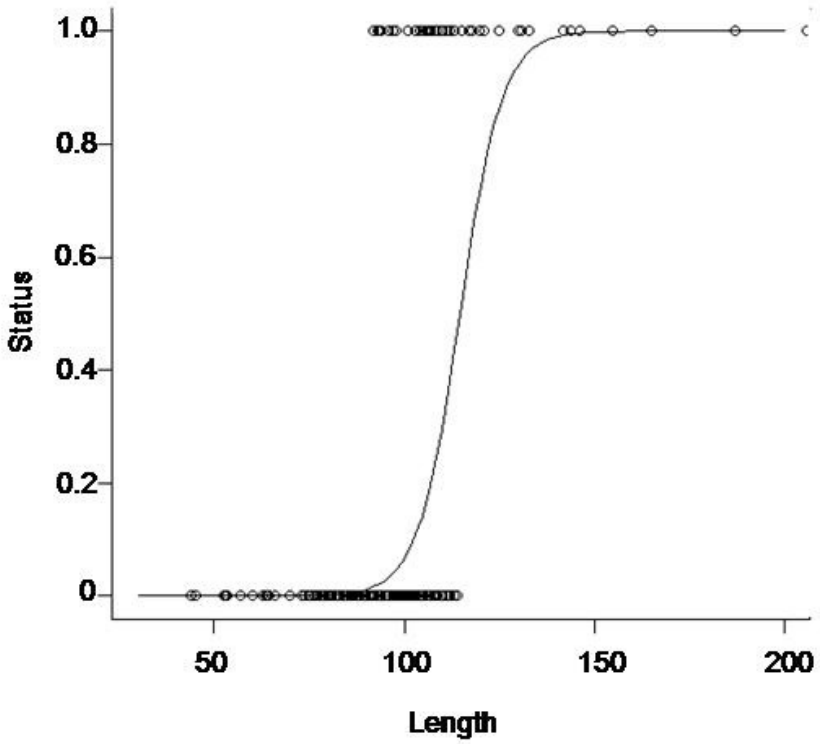

Figure 14. Logistic Fit for Length at Birth. The y axis represents the probability that an observed individual will be fetal or non-fetal dependent upon length.

(Stolen *et al*. 2002). The postnatal growth rate constant in this study is slightly higher than these reported values but is still consistent with previous predictions. The absolute growth rate and growth rate decay for bottlenose dolphins in Sarasota Bay, Florida (Read *et al*. 1993) are much lower than those values given for other regions of the Gulf. However, mother-calf pairs were excluded from this dataset, which eliminated the neonatal period of rapid growth, in effect reducing predicted growth rates.

As expected, sex differences did not manifest in early life, and growth of males and females differed mainly in the exponential rate of growth decay. Females typically achieve reproductive capacity approximately two years before males, and the asymmetry in growth is likely related to the onset of sexual maturity. Typically, populations that experience predictable, seasonal food shortages also reproduce seasonally. Females begin to store or divert resources for the preparation of reproductive activities at one or a few times of the year (Vaughan *et al*. 2000). In bottlenose dolphins, storage is related to the timing of lactation rather than conception or gestation (Kastelein *et al*. 2002), but the generalist diet of bottlenose dolphins makes it difficult to predict which seasonal food abundances are the most important relative to lactational effort. The concept of seasonal food availability warrants more investigation, particularly since bottlenose dolphin populations at similar latitudes exhibit vastly, dissimilar breeding seasonality (Urian *et al*. 1996), perhaps in response to regionally diverse prey abundances.

Table 8. Summary of Growth Rate Constants.

Male	Female	Model	N	Reference
0.16*	0.16*	Gompertz	36	Siciliano *et al*., 2007
0.73	0.77	Gompertz	36	Turner *et al*., 2006
0.72	0.77	Gompertz	199	Stolen *et al*., 2002
0.10	0.17	von Bertalanffy	174	Cockcroft and Ross, 1990
0.76	0.79	Gompertz	205	Fernandez and Hohn, 1998
0.07	0.12	Gompertz	96	Read *et al*., 1993
0.8	0.84	Gompertz	232	Present Study

*k reported as combined value for males and female

Ossification Scores and Prenatal Age Estimation

Ossification scores for bottlenose dolphin flippers failed to produce a useful gestational aging method (increased sample size may indicate a stronger correlation). However, aging may be more successful when correlated to bone density (Butti *et al*. 2007), rather than bone ossification. Development of the cetacean forelimb has been strongly correlated to life history transitions such as the onset of reproductive maturity (Galatius *et al*. 2006). However, embryonic variation is well documented in delphinids, and bony elements are often reduced or absent due to selective pressures of the aquatic environment that favor the retention of juvenile traits (Galatius *et al*. 2006, Richardson & Oelschläger 2002). The delayed or absent phalangeal epiphyseal development and the strong tendency for heterochrony in the forelimbs of prenatal delphinids makes ossification score an unreliable index of gestational age.

A number of methods have been proposed to estimate fetal age (Boyde 1980, Frazer & Huggett 1973, Huggett & Widdas 1951, Kasuya 1977, Lacave *et al*. 2004). Since no validated recording structure exists for fetal bottlenose dolphins, age must be estimated using validated growth relationships as in this study. Captive studies where reproductive timing and status are strictly controlled are extremely useful in this capacity. The most detailed examples can be found in agricultural and bovine literature. Given the phylogenetic proximity of the Order Artiodactyla to Cetacea, studies of cattle conceived using assisted reproductive technologies (ART, Correa & Zavos 1996) provide a useful model to develop cetacean fetometrics for aging purposes. For instance, crown to rump length (CRL) in fetal cattle has been used to successfully estimate prenatal age during bovine gestation. Interestingly, a significant *linear* relationship was obtained when bovine fetal biparietal diameter was regressed against crown to rump length (Riding *et al*. 2008). The linearity of this growth relationship is not surprising, especially since cows give birth to relatively precocial offspring (3, Derrickson 1992). Compelling similarities between bovine and cetacean development support growth model predictions in this study, particularly in the larger context of age-specific developmental life history strategies.

Impact of Prenatal Data on Growth Parameters

The von Bertalanffy model has been successfully used to simulate growth in a number of marine species (Robillard *et al.* 2009, Liu *et al.* 2009, Paul & Horn 2009, Tovar-Avila *et al.* 2009, Espinosa *et al.* 2008, Hwang *et al.* 2008, Hughes

et al. 2008, Leaf *et al.* 2008). Consequently, it was hypothesized that an increased sample size in this study would improve the fit at least slightly. It is interesting to note that the fit of the von Bertalanffy declined with an expanded dataset, and failed to explain growth early in life. In large measure, this is due to the high weight given to larger individuals. The theory of von Bertalanffy's growth is based on the assumption of perfect allocation, or the supposition that anabolism is equal to catabolism, and all nutrition is optimally assimilated for somatic growth (von Bertalanffy 1938). In reality, mammalian growth regimes change at sexual maturity, and at best, the von Bertalanffy growth is an optimality model (Czarnoleski & Kozlowski 1998). The Gompertz growth model is advantageous for mammalian size-at-age data because it is anchored by a "size at birth" parameter, and it accounts for resource allocation for reproduction. As growth rate decay increases, so does the proportional impact to somatic growth. Recall the Gompertz and the von Bertalanffy growth equations:

$$L_t = L_0 e^{[G/g(1-\exp(-gt))]}$$

(Laird 1966b)

$$L_t = L_\infty (1 - e^{-G/g(t-to)})$$

(von Bertalanffy 1938)

Each equation contains a growth penalty for increasing size. As age and the rate of growth decay (g) become larger, so does the cost to the growth rate constant

(G/g). In the Gompertz model, length from birth (L_0) only increases by some factor of assimilation ($e^{[G/g(1-exp(-gt))]}$). In contrast, von Bertalanffy's model implies that length at time t should be equal to some proportion of asymptotic length *assuming* that all energy is expended for somatic increase throughout life. Many mammalian species face a tradeoff between size and reproduction. For this reason, western Atlantic common bottlenose dolphin growth is better described by a Gompertz rather than a von Bertalanffy growth model, to account for reproductive growth.

The Gompertz growth model was chosen in favor of the von Bertalanffy growth model for the postnatal dataset and the pre- and postnatal dataset due to superior fit in both cases. The addition of fetal information affected Gompertz growth predictions in two ways: 1) it influenced the absolute growth rate (G) and the rate of decay (g), and 2) it demonstrated a decrease in age at asymptotic length. The comprehensive growth curve indicated that the absolute growth rate (G) for bottlenose dolphins is significantly higher than previously reported. The overall growth rate constant, k, remained unchanged throughout life, as G and g tend to fluctuate in constant proportions to one another. This indicates that while prenatal growth processes (fast initial growth and decay) differ from postnatal growth processes (slow initial growth and decay) the underlying growth regulations (G/g) help to maintain morphological proportionality as the animal ages. The commonly reported growth parameter, k, is somewhat misleading because it provides no information about the absolute growth rate (G), or the

growth rate decline (g), at time x, and these parameters become masked in the context of population comparison. For instance, the growth rate constant for postnatal individuals in this study was predicted by the model to be 0.81, but when fetal data were included, the growth rate constant decreased to 0.72. This suggests a growth discrepancy but it does not indicate in which aspects (absolute or decay rate). Despite the large growth rate constant variance (see Table 7) across geographic regions, the absolute growth rate and growth rate decay were similar to the previously reported values of Fernandez and Hohn (1998). The sensitivity of the growth rate constant to small changes limits its use in practical management. Expressing the constant as G/g instead of k is far more quantitative and pragmatic for growth assessments. This is particularly true when summarizing demographics or life history traits that may be influenced (to some degree) by intrinsic growth rates and survival strategies.

It is evident from the ultrasound data, and the model predictions that fetal growth is much faster and more influential on length-at-birth than previously thought. In fact, while sexual dimorphism was demonstrated with respect to asymptotic length, the similar lengths at birth of males and females supports the hypothesis that sex-based growth discrepancies do not manifest until well after birth mainly due to the accelerated rate of growth decay in females compared to males. The postnatal growth of small delphinids is often depicted as fast initial growth with steep decline after the first few years of life (Cockcroft & Ross 1990a, Cockcroft & Ross 1990b, Fernandez & Hohn 1998, Read *et al*. 1993, Rosas *et al*.

2003, Siciliano *et al.* 2007, Stolen 1998). The postnatal growth of bottlenose dolphins along coastal Texas is similar. In fact, the growth rate constant has changed little in recent decades (k = 0.79, Fernandez and Hohn 1998), and is similar to the growth rate constant for the Indian River Lagoon population (k = 0.77, Stolen *et al*. 2002). The postnatal curve explained asymptotic length well but not length at birth. In contrast, the pre- and postnatal growth curve indicated superior fit to length at birth and a poor fit of asymptotic length. Neither model can explain variation at all life stages along the growth curve. For instance, the length at birth was validated using three independent methodologies: a fetal model, a pre- and postnatal Gompertz model, and a logistic model fit to binomial data. All three models predicted a length at birth between 114 and 117 cm (116.6 cm, 116.3 cm, and 114.7 cm respectively). It is possible that some teeth that were aged as neonatal were in fact fetal. However, it is more likely that the model prediction of 111 cm is an underestimate of length at birth particularly given the great length variability seen in neonates. However, the combined pre- and postnatal model exhibited a poor fit in later age classes, and the decision to utilize prenatal age data strongly depends on the question of interest. If study objectives require information regarding length at birth, then a pre- and postnatal model predicts more precise information than an exclusively postnatal model. Conversely, if study objectives require information regarding age and length at sexual maturity, for example, then an exclusively postnatal model is appropriate. While the Gompertz demonstrates exceptional fit of both datasets independently,

the entire life cycle of bottlenose dolphins would be better explained by a growth model that allows for greater flexibility in model parameters.

Determinates of Cetacean Prenatal Growth

Cetaceans produce offspring of moderate independence (Derrickson 1992), however some offspring traits are more altricial than prococial. Specifically, the lactation period is prolonged in most cetaceans (Archer & Robertson 2004, Barros *et al.* 2002, Danil & Chivers 2007, Haenel 1986, Shirakihara *et al.* 2008, West *et al*. 2007). The fact that these offspring can sustain on solid foods long before weaning (e.g. Archer & Robertson 2004), suggests that the behavior may only appear altricial. It has been hypothesized that eutherian offspring that appear "outwardly" altricial may in fact develop precocial behavioral strategies more rapidly than eutherian offspring in which allometry is slanted in favor of body development. Degree of placentation *in utero* determines whether fetal brain development is facilitated by fetal anabolism or fetal extraction of maternal proteins (Elliot & Crespi 2008). Fetal determinates of growth are largely driven by the phenomenon of genomic imprinting, or the selective "silencing" of fetal genes by one parent (Reik & Walter 2001). Maternal imprinting will result in growth determinates that reduce maternal investment while paternal imprinting will result in determinates that promote greater maternal investment (Haig 2006). In other words, maternal imprinting can have antagonistic effects on fetal development.

Although the degree to which fetal cetaceans can exploit the maternal environment is unknown, an investigation of long-finned pilot whales (*Globicephala melas*) demonstrated that organochlorine intrauterine transfer from mother to fetus was only about four to ten percent of the maternal load. In contrast, depuration transfer from mother to calf was anywhere from sixty to 100 percent of the maternal load (Borrell *et al*. 1995). These results indicate that maternal investment is far more significant postnatally suggesting maternal genomic imprinting suppresses exploitation of maternal resources by the fetus. If maternal imprinting is affecting fetal growth antagonistically, then reduced growth potential in the prenatal environment selects for behavioral or social altriciality (i.e. prolonged lactation) while prolonged gestation selects for physiological precociality (i.e. independent locomotion).

Trends Associated with Offspring Precociality

A number of eutherian mammalian trends may be inferred from fast intrauterine growth followed by relatively slower postnatal growth rate. Trends among eutherian mammals that give birth to precocial young include the production of large fat stores, attainment of large size, long gestation periods, small neonatal size relative to maternal size, high encephalization quotients, and reduced investment in lactation (Eisenberg 1981). These traits are by no means ecologically crystallized and clear exceptions exist. For instance, bottlenose dolphins are known to have lactation periods that are variable in length (Wells *et al*. 2005). One

hypothesis maintains that while precocial young may nurse for extended periods, the actual nutritive value may be greatly diminished long before weaning. Pantropical spotted dolphin calves have been observed to nurse long after they could be fully sustained on solid foods (Archer & Robertson 2004). Prolonged nursing may serve to solidify parental-offspring bonds until such time that offspring have matured their foraging strategies in preparation for independent survival (Eisenberg 1981). In short, one life history trait alone is likely to be inadequate to explain a higher prenatal growth rates, and a combination of developmental strategies and ontogeny may underlie proximate causes.

The strongest selective pressures driving the production of altricial or precocial young are the predictability of food abundances, and strategies for coping with shortages (Eisenberg 1981). Because shortages inevitably arise, a female seeking to maximize reproductive output must face a tradeoff. She can either lengthen her life span or decrease her interbirth interval (Eisenberg 1981), and it appears that bottlenose dolphin females have chosen the former. Wells *et al*. (2005) determined that the intercalf interval actually lengthened over time so that young females experienced the shortest intervals and older females the longest. Furthermore, if a female "chooses" an altricial parental strategy, she is encumbered by two additional decisions that influence reproductive output; how she can hide the underdeveloped young ("nesting" behavior) and how often she should tend to them between her own foraging bouts (maternal absence from the

nest). For most large mammals, finding a cache to birth and care for offspring becomes difficult with increasing adult size, and usually prohibits the production of altricial young (Hennemann 1984). Securing a den in an aquatic environment is impossible for large, air-breathing cetaceans, so females rely on the rather developed physiology of their young to minimize costly investment, while maximizing reproductive output. Life history covariates such as large size, life span, and degree of precociality underlie the r-K selection strategies model proposed by MacArthur and Wilson (1967), and the slow-fast continuum formulated by Pianka (1970), which will be discussed in Chapter IV.

CHAPTER III

AGE AND POPULATION STRUCTURE, SURVIVORSHIP, AND MORTALITY

Introduction

Mortality and survivorship are important concepts to quantify for any population under study, particularly those with a conservation priority. Many demographers prefer to summarize data in a tabulated life table because if one value is known, the others can be deduced algebraically. Ideally, all individuals in a population cohort would be followed from birth to death, which would allow the survivorship of each age class to be measured directly. However, it is far more pragmatic to use a cross-section of deceased animals of known age, or a time-specific life table. The disadvantage to this method is that the population growth must be near constancy (r=0.00) and exhibit a stable age structure, although these assumptions may be invalid in many populations (Krebs, 1998). Stolen and Barlow (2003) estimated the intrinsic rate of increase (the assumption of stable age distribution) of bottlenose dolphins in the Indian River Lagoon System (Florida) by logarithmically regressing the number of strandings against year, then smoothing the data for each estimated growth rate. However, the assumption of stable age distribution can also be tested by constructing survivorship curves. If unexpected “inflections” occur along the curve, it is likely that a large proportion of individuals are removed or added due to age-specific mortality or recruitment (Putman and Wratten 1984).

While time-specific life tables key in on vital rates, they do not suggest causal mechanisms. Resolution of vital rates is also limited in large measure by how the age intervals are defined (Krebs 1978, Putman & Wratten 1984). Despite these limitations, life tables are particularly useful for summarizing data from populations from which little is known due to logistical difficulties in collecting data from live animals, such as marine mammals.

Mortality and Maternal Investment

High bottlenose dolphin calf mortality has been documented in many regions (Wells *et al*. 2005; Stolen and Barlow 2003). In some bottlenose dolphin communities, the phenomenon of depuration may explain higher mortality among calves. Individuals in Sarasota Bay, Florida exhibited elevated polychlorinated biphenyl (PCB) blubber concentrations, and primiparous mothers had a tendency to pass on a majority of this PCB load to their nursing calves through their milk. Interestingly, PCB blubber concentration decreases as intercalf interval increases as a function of the number of offspring produced (Wells *et al*. 2005). This finding is consistent with hypotheses regarding maternal investment in other mammalian taxa. For example, maternal care of baboon offspring increased with increasing habitat quality, suggesting that investment may be a function of environmental influences on the mother rather than the offspring (Lycett *et al*. 1998). Maternal factors are difficult to quantify *in situ*, but calf mortality is easily quantified by survivorship curves constructed from life table data, and may be a better proxy of habitat quality. Therefore, the objective of this study was to

construct a time-specific life table for bottlenose dolphins along coastal Texas using age data (see Chapter II).

The Leslie matrix is a population transition matrix that predicts population abundance in the next sequential timestep (Putman and Wratten 1984). It contains the age-specific survival rates along with fecundity values. When multiplied by the interval specific abundance vector, n_i, the product n_{x+1} provides the abundance in the next time step (Heppell *et al*. 2000). Use of transition matrices is widespread in biology (Durant *et al*. 2008, Lee *et al*. 2008, Robinson *et al*. 2008, Sadhukhan *et al*. 2008, Wallace *et al*. 2008, Zhao *et al*. 2008) because they allow fecundity and survivorship dimensions to influence one another (Putman & Wratten 1984). However, calculating fecundity using deceased animals is difficult to quantify accurately, because time-specific life tables assume that all tabulated individuals contribute to their age-specific mortality rates. Therefore, age-specific fecundity is typically not represented in time-specific life tables. However, if birth and death rates are assumed to be constant (stable), it is possible to determine the intrinsic capacity for increase, (r), by the equation:

$$N_t = N_0 e^{rt}$$

(Krebs 2001)

where N_t is the population size of individuals at time step t, and N_0 is the total population size. The sum of r_t at each time step provides the population's

intrinsic capacity for increase (r). A population becomes more stable as r approaches zero (Krebs 2001). Because male contribution to reproductive output is difficult to quantify, population analyses require the assumption that females give rise to additional productive females (Krebs 2001). Each individual should replicate itself, at least once. This replacement factor, or the population growth rate (λ), is easily calculated:

$$\lambda = e^{r}$$

(Ricklefs 2000)

If λ is equal to one, the population is perfectly replacing itself. If λ is less than one, the population will experience a decline (Ricklefs 2000).

Objectives and Hypotheses

The objectives of this study were to construct a time-specific life table (Brewer 1988, Ricklefs & Miller 2000) for males, females and the overall population to determine age specific mortality rates and survivorship of bottlenose dolphins along coastal Texas. Survivorship curves were used to test the hypothesis that calf mortality (year one) is not significantly different from juvenile (year two to five), sub-adult (year six to ten) and adult (> ten years). In addition, survivorship curves from time-specific life table data for the overall population, (and separated by females and males) were derived to determine if the population of bottlenose dolphins along coastal Texas exhibits a stable age distribution based upon the shape of the survivorship curves. If the population

exhibits a stable age distribution, survivorship will be constant through time (linear). Life tables were also used to test the hypothesis that there are no sex-based mortality differences. Last, life tables were used to test the hypothesis that the population is not stable ($r \neq 0.00$), and is not perfectly replacing itself ($\lambda \neq 1$).

Methods

Life tables were constructed from age data from two hundred eighty individuals (see CHAPTER II) from a hypothetical cohort of 1000 individuals. Tables were constructed according to sex and the overall population. All of the variables in Table 9 were calculated for each life table. A one-factor ANOVA was used to test for significant differences in the mortality rates (q_x) of each age class: calf (less than two years), juvenile (one to five years), sub-adult (six to ten years), and adult (>ten years) to determine if neonatal mortality was significantly higher than other age classes. Age classes were divided based upon previous studies of bottlenose dolphin calf mortality (Mann & Watson-Capps 2005, Neil & Holmes 2008, Stolen & Barlow 2003, Wells *et al*. 2005), weaning (Cockcroft & Ross 1990a, Connor *et al*. 2000, Peddemors *et al.* 1992, Wells *et al*. 2005, West *et al.* 2007) and reproduction (Connor *et al*. 2000, Mann *et al*. 1999, Sergeant *et al*. 1973, Urian *et al*. 1996, Wells & Scott 1990, Whitehead & Mann 2000).

Table 9. Life Table Variables.

Variable	Notation	Calculation
Age Interval	x	Based on some seasonal recording structure
Individuals in age class, x	n_x	Number of remaining individuals
Number of 1000 individuals	n_x1000	Number of individuals from a hypothetical cohort of 1000
Individuals dying in age class, x	d_x	Number of deceased individuals recovered in each age interval
Survivorship	l_x	n_{x+1}/n_x
Mortality	q_x	$(l_x-l_{x+1})/l_x$
Average population size at age interval, x	L_x	$(n_x+n_{x+1})/2$
Sum total individuals remaining at age interval, x	T_x	$\sum L_x$
Expectation of future life	e_x	T_x/L_x

(Krebs 1978, Krebs 1998, Verhoeven 1986)

A two-sample t-test was used to test for significant differences between male and female mortality rates. Survivorship curves were constructed per 1000 individuals regressed against age for the overall population, males alone, and for females alone to determine the average decline in survivorship per age interval (Caughley 1965, Krebs 2005). If no inflections were evident along the survivorship curve (i.e. if the survivorship curve was significantly linear), it was assumed that the population exhibited a stable age distribution (Putman & Wratten 1984). The intrinsic capacity for increase was calculated using tabulated life table data for all females in the sample per 1000 females. The population

growth rate (λ) was calculated using the intrinsic capacity for increase (Ricklefs & Miller 2000). Life tables, the population growth rate, and the intrinsic capacity for increase were calculated using Microsoft Office Excel (2003). All statistical analyses were conducted using SPSS v.14.0 (SPSS, Chicago, Illinois).

Results

Mortality and Survivorship

The life tables for Texas coast bottlenose dolphins are provided in Appendix A, B, and C, and include the overall life table, the female life table, and the male life table. The sex ratio (males:females) for all individuals of known sex was 127:78. Mortality of neonates was twenty-three percent in the life table for the overall population. A one-way ANOVA indicated no significant difference in mortality rates between age classes.

The data for the overall population and females and males (Figures 15 and 16) were fit with convex polynomial functions characteristic of type III survivorship (Krebs 2005). Downward type III inflections indicated an unstable age distribution. Male calf mortality was slightly greater than the overall and the female mortality of calves less than one year of age, which indicates the importance of mortality data for individuals of undetermined sex. Polynomial functions explained female and male survivorship well (ninety-four and ninety-seven percent explained variation, respectively). Male and female expectation of future life was similar initially, but male expectation appeared to decline more rapidly than female expectation until approximately twenty-five years of age.

Male expectation of future life stabilized at this time, and exhibited a slower gradual decline compared to remaining female life. Mortality did not significantly differ across sex or age class.

Intrinsic Capacity for Increase (r) and Population Growth (λ)

The intrinsic capacity for increase was -0.07 indicating a population decline over time. However, since the population distribution was left skewed in favor of neonates, the first two age classes were excluded and r was recalculated. The new value (-0.06) did not significantly differ from the prior analysis when calves were included. The population growth rate λ, was calculated to be 0.93. This indicates imperfect replacement and population decline with time. However, reduced mortality in the first two years of life was accompanied by a relatively large increase in λ. Guaranteed survival in the first ten years of life saw a three percent increase in replacement value.

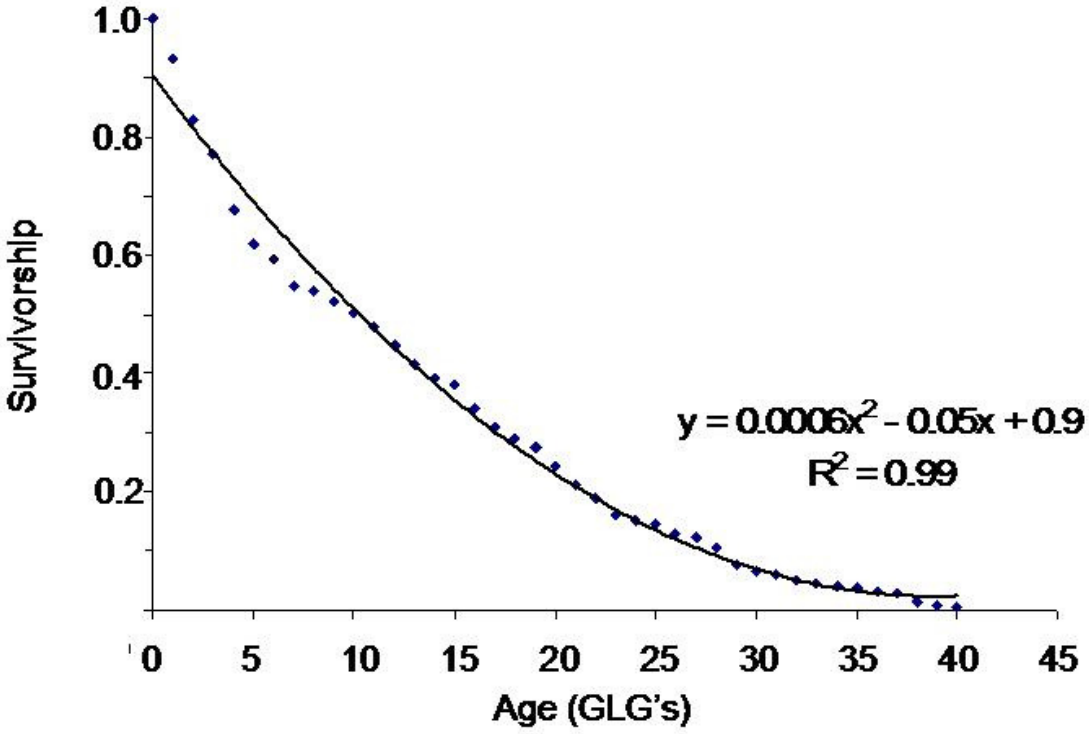

Figure 15. Overall Population Survivorship Curve.

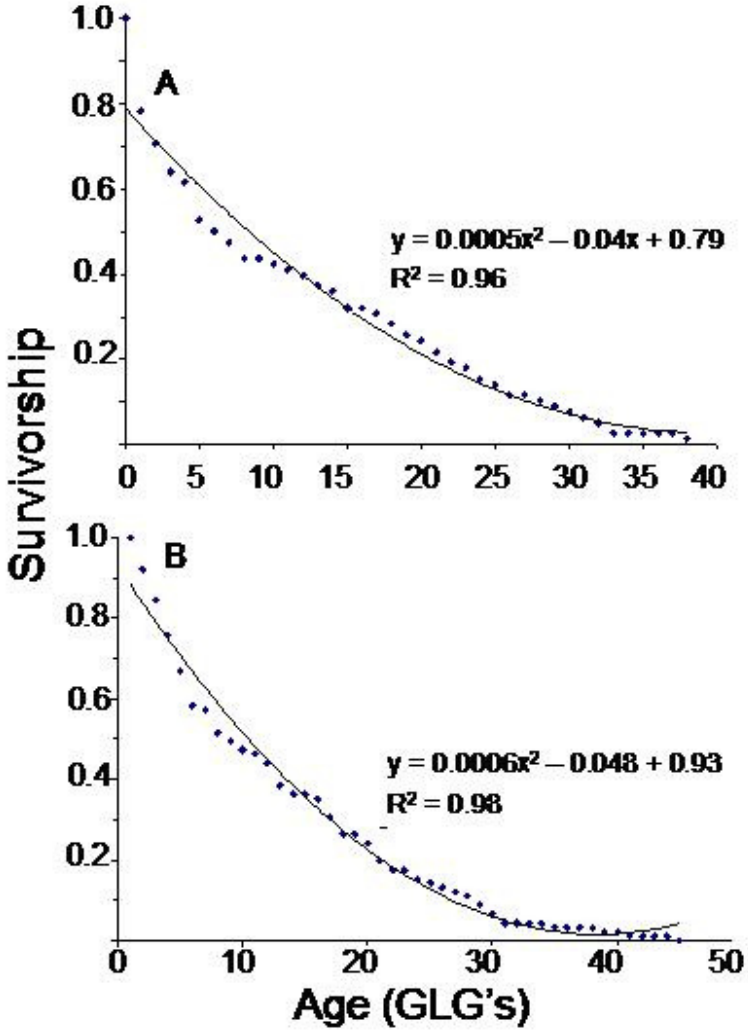

Figure 16. Female and Male Survivorship Curves. Independent survivorship curves for females (A) and males (B) fit with convex polynomial functions.

Discussion

Survivorship

High calf mortality has been documented for many regions (Cockcroft & Ross 1990b, Fernandez & Hohn 1998, Mann & Watson-Capps 2005, Mattson *et al*. 2006, Read *et al*. 1993, Sergeant *et al*. 1973, Stolen & Barlow 2003, Wells & Scott 1990). A stranding distribution for bottlenose dolphins along coastal Texas also suggests high calf mortalities. Similar patterns were evident in the survivorship curves in this study. The shape of the curves suggests a strong type III survivorship. This is uncommon for large, long-lived mammals because high losses of precocial young translate into high investment losses for the mother. A "U" shaped survivorship has been demonstrated in other bottlenose dolphin populations (Stolen 2003). Occasionally this type of survival is observed in large mammal populations where juveniles are naïve to foraging or predation factors (Brewer 1988, Ricklefs & Miller 2000). High mortality in younger age classes with a steep decline in later age classes supports the hypothesis that calves less than one year of age experienced the highest mortality rates. However, acute toxicity from commercial and industrial runoff has been suggested to be an important consideration in explaining marine mammal die-offs and population decline.

The causal mechanisms for mortalities related to organochlorine poisoning are poorly understood, but a few hypotheses have gained substantial support. Bioaccumulated brevetoxin has been correlated to higher stranding

rates as well as unusual mortality events in the Gulf of Mexico (Fire *et al.* 2008a, Fire *et al.* 2008b, Hinton & Ramsdell 2008). A second type of bioaccumulated algal byproduct, domoic acid (DA) is a metabolite produced by an algal bloom of a diatom, *Pseudo-nitzchia.* Domoic acid causes severe neurological effects in marine mammals (Bejarano *et al*. 2008), and California sea lions (*Zalophus californianus*) are documented to be particularly sensitive (de la Riva *et al*. 2009). In 2005, domoic acid toxicity was responsible for mass pregnancy failures near San Miguel Island, California. Fetal pups exhibited amniotic inflammation and lesions from brain edema resulting in spontaneous premature parturition (Goldstein *et al*. 2009). In this study, a large proportion of stranded individuals were near-term fetuses and domoic acid should be considered as a potential agent of population decline through reproductive failure during late gestation.

Polychlorinated biphenyls (PCB) from commercial runoff have been linked to high mortality of first-born calves that receive the greatest pollutant load from the mother's milk (Wells *et al*. 2004, Wells *et al*. 2005). This is consistent with trends in Matagorda Bay, Texas, where seventy-eight percent of neonatal mortality can be correlated to organochlorine poisoning from "depuration" or the passing of an organic pollutant load from mother to offspring (Schwacke *et al*. 2002). However, there are no records of direct marine mammal mortality due to PCB exposure, and the mechanism of toxicity may be indirect immunosuppression or reproductive impairment rather than acute pathology

(O'Shea 1999). For example, PCB's have been demonstrated to cause uterine lesions and decreased conception rates in mammals (Arnold *et al.* 1999, Backlin *et al.* 2003).

Male and female mortality rates are comparable over a lifetime. Because males and females do not exhibit sexual dimorphism until later in life, they are subject to the same mortality factors related to foraging and predator avoidance. Although, there was no evidence to indicate asymmetrical mortality, the bias within the sample for more males may indicate discrepancies between the *primary* sex ratio and the *operational* sex ratio. The primary sex ratio represents the proportional presence of males and females, and the operational sex ratio takes into account only those individuals that participate in successful breeding (Ricklefs & Miller 2000). For example, juvenile bottlenose dolphin males are typically solitary, have broader ranges, and fewer, successful copulations than adult males, which tend to form male-male pairs, secure smaller ranges, and interact within smaller social frameworks (Archie *et al.* 2008, Connor *et al*. 2000, Owen *et al.* 2002). These strategies appear to be correlated to male age in addition to sexual maturity, and suggest an active exclusion of younger, but sexually mature males in favor of older males that may be able to better court females. Alliances of two or even three males is common (Connor *et al*. 1992, Krutzen *et al.* 2003, Parsons *et al.* 2003, Quintana-Rizzo & Wells 2001), but ultimately only one copulation results in a successful pregnancy per courtship effort. This may effectively reduce the primary ratio of roughly 1.6:1 to an

operational sex ratio near 1:1 assuming mortality rates remain similar for both males and females over their reproductive lifetimes.

Intrinsic Capacity for Increase and Population Growth

Globally, many mammalian species are in a state of population decline due in part to habitat destruction, climate change, or both (Brook *et al.* 2003, Burger & Lynch 1995, Ceballos & Ehrlich 2002, Jones 2008, Reif *et al.* 2008, Thomas *et al.* 2004). Any species has the potential for exponential increase given unlimited resources and a stable age distribution (Brewer 1988). This is rarely the case except in instances of recent access to new habitats. If a population lacks the resources to grow exponentially ($r = 0.00$), λ should be equal to one in order for the population to maintain stasis. In the present study, the population of bottlenose dolphins along coastal Texas is only replacing itself at ninety-two percent of its biotic potential ($\lambda = 0.92$). However, many large-bodied mammal life cycles are complex and include transitional stages that present a greater liability to population growth over time. For example, the mortality data from this study indicated that when calves were guaranteed survival to reproductive age, population growth rate increased three percent. However, guaranteed survivorship past reproductive age (ten years) had minimal impact on population growth rate.

Population growth rate does not necessarily indicate population status. Culling activity from a hunted population of cougars (*Puma concolor*) encouraged compensatory immigration, but because $\lambda = 1.00$, regional

population decline was not initially apparent from analyses (Robinson *et al*. 2008). North Atlantic harbor porpoises (*Phocoena phocoena*) exhibited a population growth rate greater than one even though incidental mortality from gillnet fisheries likely exceeded critical thresholds established for the population (Robinson *et al*. 2008). By comparison, the population growth rate of Texas coast bottlenose dolphins is low, but without detailed density compensatory information, it is difficult to predict the long-term impact to the population.

Determinates of Population-Level Behavior

A number of predictive models have been proposed to explain a range of population behaviors. The r-K selection strategies model (MacArthur & Wilson 1967) was rejected when investigators found that some traits of r or K selected species could simply be correlated, to some degree, and most animals fell along a continuum between competition and resource instability (Pianka 1970). Life history traits covary as much with one another as they do with competitive selection or habitat stability. Investigators used principle component analysis (PCA) to demonstrate that life history variation could be more accurately characterized along three axes: body size, the fast-slow continuum, and fecundity (Dobson & Oli 2007). Under this model, most other life history traits such as degree of offspring precociality, length of lactation, and gestation length represent simple correlates, but explain little regarding life history variation among mammals. Two of the three axes (body size and lifespan) can be obtained from basic demographic information collected from stranded bottlenose

dolphins. Fecundity is far more difficult to measure without employing long-term, mark-resight methods (Hadley *et al.* 2007, Wells & Scott 1990) or seasonal information on the reproductive status of individuals. An alternative life history model, known as the "bet-hedging" model maintains fecundity as a primary impetus, while parental investment and generation time drive the second and third axes. "Bet-hedging" places little emphasis on body size and abandons any perceived tradeoff between body size and reproductive output (Winemiller 1992). However, "bet-hedging" says nothing of density-dependence or resource availability. Instead, it suggests how an organism should respond to environmental change. Bottlenose dolphins exhibit substantial parental investment, and long generation times. If low fecundity is assumed based upon calf precociality and mortality rates (which may or may not be supported by empirical data), then their life history strategy could likely be identified as an intermediary between "equilibrium" (the optimal strategy for stable environments) and "periodic" (the optimal strategy for seasonally patchy environments).

In this respect, estimates of growth and population structure provide limited detail without fecundity data. However, basic demographic information enables reasonable predictions about population behavior and justifications for future studies. For instance, low intrinsic capacity for increase is generally correlated with large, long-lived mammals, which experience seasonally available, but predictable food resources. Although female bottlenose dolphins give birth synchronously in the wild, calving season is regionally dissimilar.

Timing of calf births is unrelated to latitudinal gradients, and investigators hypothesize that reproduction is instead correlated with regionally and temporally available prey (Urian *et al*. 1996). Peak energy storage in bottlenose dolphin females has been observed in late gestation and early lactation (Urian *et al*. 1996, West *et al*. 2007). If seasonality is regionally known, the period of calving presents an optimal time to map prey species distributions and compare them with distributions on wider geographic scales.

Another useful correlate for population analysis is the presence of well-developed young. In this study, the most dramatic growth was demonstrated *in utero* and long gestation time facilitated an elevated growth rate (Derrickson 1992). These results are intriguing because the presence of precocial young may explain a low reproductive output. Presumably, well-developed offspring translate to greater prenatal than postnatal investment. A highly developed neonate can expect a lower probability of mortality and substantially less contribution from the mother (Eisenberg 1981). However, stranding patterns suggest a high probability of neonatal mortality relative to development. This demonstrates that growth and mortality estimates are only predictive in a vacuum, that is, if environmental conditions remain stable. In contrast, estimates of parameter elasticity indicate proximate factors that influence population-level behavior (Heppell *et al*. 2000). For example, given a set of parameterized demographic data, the parameter that exhibits the highest elasticity (i.e. the parameter that changes proportional survival the most) should be the focus of

management efforts (Heppell *et al*. 2000). However, reproductive information must be well understood to produce optimal output. It is difficult, if not impossible, to validate these predictions or calculate scalar indices that are useful for management purposes, without information on birth rates from a large population of live individuals or reproductive information from the ovaries of stranded females.

CHAPTER IV

CONCLUSIONS

The results of this study demonstrate that bottlenose dolphins along coastal Texas conform to a number of eutherian mammalian trends of age, growth, and life history strategies. Specifically, they exhibit a fast fetal growth rate consistent with the production of precocial young, are long-lived, and experience lengthened gestation periods. A number of predictions can be made based upon this information. The population is likely subject to a low net reproductive output (Vaughan *et al*. 2000), reduced lactational investment (with compounding social variables, Eisenberg 1981), and is extremely vulnerable to unpredictable environmental change (Eisenberg 1981) or variation in annual fecundity (Hennemann 1984). Although bottlenose dolphins share many of these life history traits, it is difficult to verify which traits drive others.

The sample demographics demonstrate expected trends associated with stranding data. The left skewed distribution may not be representative of the true age distribution of bottlenose dolphins along coastal Texas. Despite the predominance of neonates present in the sample, the length-at-age growth curve still demonstrated considerable length variability. Postnatal growth is impacted by a number of variables that may have greater explanatory power in a multivariate framework. In addition, male and female growth patterns are similar, but not fully explained by a standard growth rate constant. Instead, absolute

rates indicate that length accretion is similar, but the rate of exponential growth decay results in the significant sexual dimorphism with respect to length.

Fetal length-at-age was best explained by a linear function. Fetal length and biparietal diameter demonstrate an isometric relationship in the latter part of gestation. The growth index shows very little variation across the sample. This is to be expected, since the embryonic phase is a period of organ system development (Sterba *et al*. 2000), and the fetal phase is a period of organ system elaboration. Bottlenose dolphin *intrauterine* growth occurs in a stable environment relative to early postnatal growth. This was evidenced by the low variability in the prenatal portion of the length-at-age curve relative to the postnatal portion. This led to observable variation in the predicted length at birth value that was better resolved using a pre- and postnatal length-at-age curve, which was validated using two additional independent methodologies. These results supported the hypothesis that a combined pre- and postnatal length-at-age model predicted a more precise length at birth value. However, addition of prenatal data caused the Gompertz growth model to underestimate the true asymptotic length, and reduced observable sex-related size differences. It is clear that model choice is critical to estimating precise parameters of interest, and a novel growth model may reconcile these shortcomings.

Life tables indicated no significant difference in mortality by sex despite the fact that the sex ratio indicated more males in the sample. The high number of males may not be representative of reproductively active males, which may

influence an operational sex ratio. Survivorship was characterized by high losses in early life and lower losses in later life. In reality, mortality risk likely increases as animals approach senescence, which produces the characteristic "U-shaped" survivorship curve (Stolen and Barlow 2003). However, in this study, it was impossible to make inferences regarding competing mortality risks because information regarding fecundity was not available over a wide range of individuals.

The high neonate mortality observed in this study was not significantly different from that of other maturity classes, but still depressed the population growth rate. It is possible that this in an artifact of utilizing stranding data to reconstruct age distributions, or that the estimated population growth rate is not indicative of population decline but rather population regulation to maximal carrying capacity. However, this population is vulnerable due to its low capacity for increase ($r<0.00$), which limits the population's ability to rebound following environmental change, and may present a conservation concern in the future.

Recommendations for Future Work

Bottlenose dolphin population dynamics are poorly described in the western Gulf of Mexico. In large part, this is due to the lack of annual abundance estimates and reproductive information. These endeavors involve extensive training, time, and financial investment. However, the Texas Marine Mammal Stranding Network has the benefit of a large volunteer base including a percentage of students enrolled at Texas A&M University at Galveston. This

unique affiliation promotes an environment for accessible and mutually beneficial internship programs that would require minimal infrastructure provided that, university affiliates in conjunction with stranding network personnel engage in active identification and recruitment of exemplary students.

Future investigations should focus on datasets that include the long-term analysis of age, reproductive status, and stomach contents with reference to reproductive state. Age estimates enable age-specific mortality and survivorship predictions, and retrospectively indicate possible ecosystem perturbations. Fecundity estimates in conjunction with age data provide information such as age at first reproduction, intercalf intervals, and enable direct calculations of the population growth rate. Stomach content analysis with reference to seasonality can indicate patterns in energy allocation. Bottlenose dolphins prey upon a number of commercially managed fishery species, and regulatory priorities may have direct consequences to bottlenose dolphin communities. For example, in 2008, the National Marine Fisheries Service announced restrictive guidelines for the recreational red snapper (*Lutjanus campechanus*) fishery including a mandate to shorten the fishing season in federal waters (NMFS 2008a). However, among gulf coast states, only Florida and Texas failed to initiate similar guidelines in state waters in 2007. Furthermore, Texas maintained year-round recreational red snapper fishing and a higher daily bag limit (NMFS 2008a). Another prey species, king mackerel (*Scomberomorus cavalla*) remains completely restricted in federal waters (NMFS 2008b). It is unclear how annual

fishery guidelines influence distributions, abundances, or reproductive seasonality of regional predators. Such data would provide further insight into population viability, growth, and parameter elasticity, and promote efficient and timely population mitigation planning.

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APPENDIX A

POPULATION LIFE TABLE

x	n_x	n_x1000	d_x	l_x	q_x	L_x	T_x	e_x
0	280	1000	63	1.00	0.23	248.50	2914.00	11.73
1	217	931	15	0.93	0.07	209.50	2665.50	12.72
2	202	829	22	0.83	0.11	191.00	2456.00	12.86
3	180	770	13	0.77	0.07	173.50	2265.00	13.05
4	167	677	20	0.68	0.12	157.00	2091.50	13.32
5	147	618	13	0.62	0.09	140.50	1934.50	13.77
6	134	594	5	0.59	0.04	131.50	1794.00	13.64
7	129	548	10	0.55	0.08	124.00	1662.50	13.41
8	119	539	2	0.54	0.02	118.00	1538.50	13.04
9	117	521	4	0.52	0.03	115.00	1420.50	12.35
10	113	502	4	0.50	0.04	111.00	1305.50	11.76
11	109	479	5	0.48	0.05	106.50	1194.50	11.22
12	104	447	7	0.45	0.07	100.50	1088.00	10.83
13	97	415	7	0.41	0.07	93.50	987.50	10.56
14	90	392	5	0.39	0.06	87.50	894.00	10.22
15	85	382	2	0.38	0.02	84.00	806.50	9.60
16	83	341	9	0.34	0.11	78.50	722.50	9.20
17	74	309	7	0.31	0.09	70.50	644.00	9.13
18	67	290	4	0.29	0.06	65.00	573.50	8.82
19	63	276	3	0.28	0.05	61.50	508.50	8.27
20	60	244	7	0.24	0.12	56.50	447.00	7.91
21	53	212	7	0.21	0.13	49.50	390.50	7.89
22	46	189	5	0.19	0.11	43.50	341.00	7.84
23	41	161	6	0.16	0.15	38.00	297.50	7.83
24	35	152	2	0.15	0.06	34.00	259.50	7.63
25	33	147	1	0.15	0.03	32.50	225.50	6.94
26	32	129	4	0.13	0.13	30.00	193.00	6.43
27	28	124	1	0.12	0.04	27.50	163.00	5.93
28	27	106	4	0.11	0.15	25.00	135.50	5.42
29	23	78	6	0.08	0.26	20.00	110.50	5.53
30	17	65	3	0.06	0.18	15.50	90.50	5.84
31	14	60	1	0.06	0.07	13.50	75.00	5.56
32	13	51	2	0.05	0.15	12.00	61.50	5.13
33	11	46	1	0.05	0.09	10.50	49.50	4.71
34	10	41	1	0.04	0.10	9.50	39.00	4.11
35	9	37	1	0.04	0.11	8.50	29.50	3.47
36	8	32	1	0.03	0.13	7.50	21.00	2.80
37	7	28	1	0.03	0.14	6.50	13.50	2.08
38	6	14	3	0.01	0.50	4.50	7.00	1.56
39	3	9	1	0.01	0.33	2.50	2.50	1.00

Cont'd

x	n_x	n_x1000	d_x	l_x	q_x	L_x	T_x	e_x
40	2	5	1	0.00	0.50	1.50	4.00	2.67
41	1	5	0	0.00	0.00	1.00	5.00	5.00
42	1	5	0	0.00	0.00	1.00	6.00	6.00
43	1	5	0	0.00	1.00	7.00	7.00	7.00
44	1	5	1	0.00	1.00	0.50	7.00	15.00

APPENDIX B

FEMALE LIFE TABLE

x	n_x	n_x1000	d_x	l_x	q_x	L_x	T_x	e_x
0	78	1000	17	1.00	0.22	69.50	854.00	12.29
1	61	983	6	0.78	0.10	58.00	784.50	13.53
2	55	977	5	0.71	0.09	52.50	726.50	13.84
3	50	972	2	0.64	0.04	49.00	674.00	13.76
4	48	970	7	0.62	0.15	44.50	625.00	14.04
5	41	963	2	0.53	0.05	40.00	580.50	14.51
6	39	961	2	0.50	0.05	38.00	540.50	14.22
7	37	959	3	0.47	0.08	35.50	502.50	14.15
8	34	956	0	0.44	0.00	34.00	467.00	13.74
9	34	956	1	0.44	0.03	33.50	433.00	12.93
10	33	955	1	0.42	0.03	32.50	399.50	12.29
11	32	954	1	0.41	0.03	31.50	367.00	11.65
12	31	953	2	0.40	0.06	30.00	335.50	11.18
13	29	951	1	0.37	0.03	28.50	305.50	10.72
14	28	950	3	0.36	0.11	26.50	277.00	10.45
15	25	947	0	0.32	0.00	25.00	250.50	10.02
16	25	947	1	0.32	0.04	24.50	225.50	9.20
17	24	946	2	0.31	0.08	23.00	201.00	8.74
18	22	944	2	0.28	0.09	21.00	178.00	8.48
19	20	942	1	0.26	0.05	19.50	157.00	8.05
20	19	941	2	0.24	0.11	18.00	137.50	7.64
21	17	939	2	0.22	0.12	16.00	119.50	7.47
22	15	937	1	0.19	0.07	14.50	103.50	7.14
23	14	936	2	0.18	0.14	13.00	89.00	6.85
24	12	934	1	0.15	0.08	11.50	76.00	6.61
25	11	933	2	0.14	0.18	10.00	64.50	6.45
26	9	931	0	0.12	0.00	9.00	54.50	6.06
27	9	931	1	0.12	0.11	8.50	45.50	5.35
28	8	930	1	0.10	0.13	7.50	37.00	4.93
29	7	929	1	0.09	0.14	6.50	29.50	4.54
30	6	928	1	0.08	0.17	5.50	23.00	4.18
31	5	927	1	0.06	0.20	4.50	17.50	3.89
32	4	926	2	0.05	0.50	3.00	13.00	4.33
33	2	924	0	0.03	0.00	2.00	10.00	5.00
34	2	924	0	0.03	0.00	2.00	8.00	4.00
35	2	924	0	0.03	0.00	2.00	6.00	3.00
36	2	924	0	0.03	0.00	2.00	4.00	2.00
37	2	924	1	0.03	0.50	1.50	2.00	1.33
38	1	923	1	0.01	1.00	0.50	0.50	1.00

APPENDIX C

MALE LIFE TABLE

x	n_x	n_x1000	d_x	l_x	q_x	L_x	T_x	e_x
0	127	1000	36	1.00	0.28	961.54	11532.97	11.99
1	91	923	7	0.92	0.08	884.62	10571.43	11.95
2	84	846	7	0.85	0.08	802.20	9686.81	12.08
3	77	758	8	0.76	0.10	714.29	8884.62	12.44
4	69	670	8	0.67	0.12	626.37	8170.33	13.04
5	61	582	8	0.58	0.13	576.92	7543.96	13.08
6	53	571	1	0.57	0.02	543.96	6967.03	12.81
7	52	516	5	0.52	0.10	505.49	6423.08	12.71
8	47	495	2	0.49	0.04	483.52	5917.58	12.24
9	45	473	2	0.47	0.04	467.03	5434.07	11.64
10	43	462	1	0.46	0.02	450.55	4967.03	11.02
11	42	440	2	0.44	0.05	412.09	4516.48	10.96
12	40	385	5	0.38	0.13	373.63	4104.40	10.99
13	35	363	2	0.36	0.06	362.64	3730.77	10.29
14	33	363	0	0.36	0.00	357.14	3368.13	9.43
15	33	352	1	0.35	0.03	329.67	3010.99	9.13
16	32	308	4	0.31	0.13	285.71	2681.32	9.38
17	28	264	4	0.26	0.14	263.74	2395.60	9.08
18	24	264	0	0.26	0.00	252.75	2131.87	8.43
19	24	242	2	0.24	0.08	219.78	1879.12	8.55
20	22	198	4	0.20	0.18	186.81	1659.34	8.88
21	18	176	2	0.18	0.11	175.82	1472.53	8.38
22	16	176	0	0.18	0.00	164.84	1296.70	7.87
23	16	154	2	0.15	0.13	148.35	1131.87	7.63
24	14	143	1	0.14	0.07	137.36	983.52	7.16
25	13	132	1	0.13	0.08	126.37	846.15	6.70
26	12	121	1	0.12	0.08	115.38	719.78	6.24
27	11	110	1	0.11	0.09	98.90	604.40	6.11
28	10	88	2	0.09	0.20	76.92	505.49	6.57
29	8	66	2	0.07	0.25	54.95	428.57	7.80
30	6	44	2	0.04	0.33	43.96	373.63	8.50
31	4	44	0	0.04	0.00	43.96	329.67	7.50
32	4	44	0	0.04	0.00	43.96	285.71	6.50
33	4	44	0	0.04	0.00	38.46	241.76	6.29
34	4	33	1	0.03	0.25	32.97	203.30	6.17
35	3	33	0	0.03	0.00	32.97	170.33	5.17
36	3	33	0	0.03	0.00	32.97	137.36	4.17
37	3	33	0	0.03	0.00	27.47	104.40	3.80
38	3	22	1	0.02	0.33	21.98	76.92	3.50
39	2	22	0	0.02	0.00	16.48	54.95	3.33
40	2	11	1	0.01	0.50	10.99	38.46	3.50
41	1	11	0	0.01	0.00	10.99	27.47	2.50

Cont'd

x	n_x	n_x1000	d_x	l_x	q_x	L_x	T_x	e_x
42	1	11	0	0.01	0	10.99	16.48	1.5
43	1	11	0	0.01	0	5.49	5.49	1
44	1	0	1	0	1	0	0	--

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